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THE CRANIAL MYOLOGY
AND OSTEOLOGY OF
DICOTYLES TAJACU,
THE COLLARED PECCARY,
AND ITS BEARING ON
CLASSIFICATION

MICHAEL O. WOODBURN

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SOUTHERN CALIFORNIA
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THE CRANIAL MYOLOGY AND OSTEOLOGY OF *DICOTYLES TAJACU*, THE COLLARED PECCARY, AND ITS BEARING ON CLASSIFICATION

MICHAEL O. WOODBURN¹

ABSTRACT: The cranial myology of the collared peccary is described with emphasis on the facility with which muscle attachments are determinable from remnant scars on the cleaned cranium. Individual variation with respect to the major muscle scars is noted over a range of 135 crania.

The cranial and dental osteology of the collared peccary is compared with that of the white lipped peccary. Individual variation within each sample is recorded in the text and in tabular form.

Features of the snout and zygomatic arch are found to be of value in determining the paleontological associates of each living species. The white lipped peccary is a member of a broad lineage including *Mylohyus* (late Pleistocene of North America) and *Platygonus* (*Brasiliochoerus*) *stenocephalus* (Lund, 1880) (late Pleistocene of Brazil). The line of descent common to these three peccaries can probably be traced back through *Prosthennops niobraren-sis* Colbert, 1935, to *Dyseohyus fricki* Stock, 1937. Removal of "*Platygonus*" (*B.*) *stenocephalus* from the genus *Platygonus* is advocated.

The collared peccary is considered to be broadly related to *Platygonus*. Closest resemblance is shown to *P. compressus* Le Conte, 1848, but *P. cumberlandensis* Gidley, 1920, and *P. (Parachoerus) carlesi* Rusconi, 1931, from the late Pleistocene and early Recent of South America are other members of this group.

The two broad groups thus described seem to have been separate entities since early Pliocene time. The morphological distinctions between the two living peccaries have historical significance and it is concluded that two separate genera are represented. The collared peccary is *Dicotyles tajacu* (Linnaeus, 1758); the white lipped peccary is *Tayassu pecari* Fischer, 1814.

INTRODUCTION

The generic allocation of the living peccaries has fluctuated widely ever since the collared peccary was named by Linnaeus in 1758. The white lipped species was named by Fischer in 1814 and subsequent workers have almost invariably differed, not only in their opinion as to whether the two species should be placed in the same genus or in separate genera, but also as to the names which should apply in either alternative. Singularly or collectively, the modern peccary species have been variously allocated to *Tayassu*, *Dicotyles*, *Pecari*, *Notophorous* or *Tagassu* (see Table 14).

A recent examination of the cranial myology of the collared peccary, the results of which are presented here, has occasioned a review of the problem. Although it was not possible to undertake a dissection of the rarer white lipped peccary, comparison of the cranial osteology of the two species suggests that features of their masseteric and facial musculature are quite different. These differences are of such magnitude as to suggest that the past evolution of the two species occurred along discrete lineages. An investigation of the fossil record suggests that these

lineages have probably been distinct and autonomous since at least early Pliocene time.

An investigation of the cranial osteology and dental morphology of the two species is presented, with emphasis on the individual variation observed within each species. Sixty-five cranial, mandibular and dental measurements, taken from a large sample, are statistically summarized for each species. It is intended that the range of variation thus documented for the Recent animals will be used as a uniformitarian "yardstick" when judging the content of fossil species in future work.

The two living peccaries can be differentiated by at least 28 cranial and dental characters. Both Recent forms possess a number of features which are more primitive than those seen in species of such Pleistocene genera as *Mylohyus* and *Platygonus*. *Prosthennops* and *Mylohyus* are generally considered to be more closely related to each other than either is to *Platygonus* and, although all the fossil evidence is not yet in, the white lipped peccary seems basically related to the *Prosthennops* — *Mylohyus* "lineage." The collared peccary is more closely aligned with *Platygonus*. The status of these three fossil genera is currently being reviewed and it seems likely that the

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familiar concepts of *Platygonus* and *Prosthennops*, at least, will become altered to some extent. For the purposes of this report, however, these names will be used largely in the conventional manner.

It is my opinion that the morphological distinctions which can be observed in the crania of the two living peccaries are such as to warrant their being placed in separate genera. Paleontological evidence, while incipient at this stage, seems to corroborate such a procedure, and suggests that the modern peccaries are primitive members, with some additional specializations, of two distinct, relatively long-lived lineages.

As will be developed below, the white lipped peccary should be known as *Tayassu pecari*, the collared peccary as *Dicotyles tajacu*. In the interests of clarity and convenience, these taxa will be utilized throughout the text, the justification for such usage being presented cumulatively.

Acknowledgments

This report stems from a project involving a revision of the early Tertiary Tayassuidae which was being jointly undertaken by the author and the late R. A. Stirton, of the Museum of Paleontology, University of California, Berkeley. I am indebted to Dr. Stirton for encouraging my participation in the latter project and for his suggestion that a dissection of the cranium of the collared peccary be made. Appreciation is also extended to Dr. T. E. Downs, Director of Earth Sciences, Los Angeles County Museum of Natural History, for allowing us to study and illustrate specimens under his care. Sincere thanks are also given to Dr. R. H. Van Gelder, Department of Mammalogy, and Dr. M. C. McKenna, Department of Vertebrate Paleontology, American Museum of Natural History, for permission to examine specimens under their jurisdiction. In particular, permission to examine peccary material in the Frick Collection of the American Museum of Natural History and the support of Dr. McKenna in this and other endeavors was invaluable. In addition, generous financial assistance from the Frick Laboratory enabled me to spend the summer of 1966 studying fossil peccaries in its collections and during that time some of the observations used in this report were made. Some of the costs of publication were defrayed by an Intramural Grant from the Academic Senate, University of California, Riverside. This is gratefully acknowledged.

All illustrations were prepared by me. Abbreviations which apply to specimens discussed in the text are: A.M.N.H. (M.), Department of Mammalogy, American Museum of Natural History.

Definitions

Length from the anterior tip of I^1 to the rear of the condyles: This dimension (Tables 2,8) consists of two measurements; that from the tip of I^1 to the rear of M^3 and from M^3 to the point at which a plane perpendicular to that of the palatal surface intersects the rear of the condyles. In spite of the dual nature of the total dimension, mechanical error is probably less than 3 per cent.

Length of the diastema from C^1 to P^2 : This is the distance from the rear edge of the alveolus of C^1 to the anterior edge of that of P^2 , as measured parallel to the palatal plane (Tables 2,8).

Width between the alveoli of P^2 : The dimension (Tables 2 and 8) is taken between the lingual edges of the anterior root of P^2 .

Width between the alveoli of M^3 : This is transverse distance between the lingual edges of the alveoli of the anterolingual root of M^3 . In some instances the dorsomedial slant of this root coupled with the very thin bone of the adjacent palate causes the alveolus in question to extend farther lingually than usual. Variability thus introduced into this measurement could be as much as 15 per cent (Tables 2,8).

Least width of the rostrum behind the canines: The measurement, made from the ventral aspect of the cranium, is the least transverse dimension of the rostrum measured at the level of the dorsal lip of the buccinator fossa in *Dicotyles tajacu* (Table 2) and at the point of greatest constriction of the lateral expansion of the palate in the diastemal area of *Tayassu pecari* (Table 8). The point to be stressed is that in *D. tajacu* the measurement is taken above the level of the palatal surface, not at the diastemal crests.

Height from the condyles to the nuchal crest: The measurement is taken in the plane perpendicular to that of the palatal surface. Ventrally the calipers rest on the ventral edge of the condyles; dorsally they meet the sagittal plane of the cranium either at or as much as 10 mm. anterior to the inion (Tables 2,8).

Breadth across the zygomatic arches: This dimension is also taken from the ventral aspect of the cranium. It represents the greatest transverse diameter of the cranium at the zygomatic arches, usually at or slightly anterior to the anterior edge of the glenoid fossa (Tables 2,8).

Breadth between the postorbital processes of the frontals: This parameter is measured from the dorsal aspect with the calipers resting on the lateral surface of the postorbital processes (Tables 2,8).

Length and width of the upper incisors: This measurement represents the greatest length of the tooth, parallel to the plane of the palatal surface, between its anterolingual and posterolingual edges.

The width is taken in the same plane as the length, but perpendicular to it. Because of difficulties encountered in making these measurements and because of variations caused by tooth wear, only the simplest statistical summary was made (Tables 3,9).

Length and width of the lower incisors: For I_1 and I_2 the length was taken in an anteromedial direction across the ventrolabial base of the enamel. The width was taken posterodorsally, through the body of the tooth, in a plane perpendicular to that used for the length. I_3 is oriented longitudinally so that its dimensions can be measured in the usual way. Limited statistical summaries were made of the lower incisor dimensions for the same reasons as given above and because I_3 is highly variable (Tables 3,9).

Length and width of the canines: The length of both upper and lower canines can be made along the cross sectional axis of the tooth at the base of the enamel. The width was measured perpendicular to this. Even though the greatest width of the upper canine occurs at the anterior portion of the tooth, it seems to be essentially unaffected by tooth wear. The width of the lower canine is also unaffected by wear, although the length of both teeth is decreased as wear progresses (Tables 4,10).

Length from I^1 to M^3 : This measurement was taken directly, from the anterior tip of I^1 to the rear of M^3 . Additional variability was probably introduced into the results (Tables 5,11) because of wear between adjacent members of the cheek tooth series and because of occlusal wear on I^1 .

Length and width of the upper cheek teeth: These results (Tables 5,11) are obtained in the usual way. The length is the greatest longitudinal dimension of the tooth, taken somewhat above the base of the enamel. For the upper premolars, the direction of measurement is aligned slightly anteromedially; for the molars it is roughly parallel to the long axis of the cranium. The width is measured perpendicular to the length, across the widest part of the tooth.

Length from I_1 to the condyles: This dimension (Tables 6,12) is the sum of two measurements: I_1 to M_3 length, and that from the rear of M_3 to the rear of the condyles. Mechanical error introduced by this method is probably less than 5 per cent.

Length of the diastema between C_1 and P_2 : The results are given in Tables 6 and 12. The measurement was taken from the rear of the alveolus of C_1 to the anterior alveolus for P_2 .

Depth from the tip of the coronoid process to the angle of the mandible: The measurement may be taken directly with the jaws of the calipers oriented essentially vertically. The results are presented in Tables 6 and 12.

Depth below P_2 : With the calipers oriented as in

the previous measurement, the depth (Tables 6,12) is taken from the edge of the anterior alveolus of P_2 to the ventral edge of the ramus directly below. A certain amount of additional variation results from the fact that the alveolus of P_2 occasionally extends down toward the diastemal region for as much as 5 mm.

Depth below the rear of M_1 : The orientation of the calipers is the same as above. Possible mechanical error of about 5 per cent may be introduced because of the necessity of estimating the point at which the ventral edge of the mandible would strike the lower jaw of the calipers. In this orientation the lower point of the calipers can project only slightly medial to the lateral surface of the mandible (Tables 6,12).

Width between the alveoli of P_2 : This is the transverse distance between the inner edges of the anterior alveoli of P_2 (Tables 6,12).

Width between the alveoli of M_3 : The measurement (Tables 6,12) is determined in a manner analogous to that described above.

Width between the condyles: The points of the calipers are placed between the inner tips of the condyles (Tables 6,12).

Length, P_2 to M_3 : This is the greatest longitudinal dimension of the lower cheek tooth series. The results are shown in Tables 7 and 13.

Length and width of the lower cheek teeth: The length is the greatest anteroposterior diameter of the tooth; the width is the greatest transverse diameter (Tables 7,13).

The Species of *Dicotyles*

During the early 1900's when many collections of Recent mammals were being established, a number of peccary species were proposed (see Miller, 1924, pp. 481-483 for a list). Most of these belonged to the *angulatus* group within the collared peccaries; the white lipped peccary has rarely been known by more than one species name. More recently, however, the number of specific names for the collared peccary has been reduced to one, commonly *Pecari tajacu* or *Tayassu tajacu* (compare Miller and Kellogg, 1955, pp. 792-795 with Hall and Kelson, 1959, pp. 994-999). My own observations on specimens in the collections of the Department of Mammalogy of the American Museum of Natural History would tend to corroborate this practice. While some specimens from Mexico and the southwestern United States labelled *Tayassu angulatus* (Cope, 1889) show a tendency toward increased hypsodonty of the premolar dentition in general and in particular of the anterior moiety of the teeth relative to the posterior moiety, or heel, other specimens of this "species" are not specialized to such an extent. Also, a few

specimens of *Dicotyles tajacu* from Colombia are specialized as described above, but most are not. In summary, during the course of this study I observed no character or suite of characters by which the former "species" of *Dicotyles* could be reliably validated. As far as can be determined from the available cranial and dental material, the osteological and dental variation in collared peccary occurs gradually from one portion of its geographic range to another, and, at least for the purposes of this study is considered as being contained within a single species.

MYOLOGICAL DESCRIPTION

In the following section the cranial myology of a single adult specimen of *Dicotyles tajacu* is described. It was not possible to perform a series of myological dissections and, as a result, an evaluation of the influence of individual and population variation on the development of the various muscles cannot be made. The terminology and format followed below is based on, but slightly modified from that in Sisson and Grossman (1953) as this reference affords a convenient standard. The names applied in the following description are based on the topographic position of the muscle in question and the position of its origin or insertion. Tracing the nervous and vascular associates of a given muscle was not undertaken. Homology of a particular muscle in the peccary to one found in the horse, ox, pig, or dog cannot be conclusively demonstrated.

Cutaneous Muscles

* **Cutaneous** (Fig. 1). This is a flat sheet of muscle extending from the superficial aspect of the neck

onto the posterolateral part of the face. From the nuchal ligament, the muscle extends anterolaterally behind and over the posterior auricular muscles and connects to deep fascia at the ventral and posterior base of the ear. Anteriorly, the muscle attaches to fascia adherent to the posterior surface of the zygomatic arch. The muscle leaves the arch ventral to the eye, attaching to fascia at the rear of M. zygomaticus, then continues anteroventrally below M. buccinator and fascia lying on the lateral aspect of the mandible. After wrapping around the ventral edge of the mandible, the left half of M. cutaneus meets the sheet from the opposite side at the median raphe found along the ventral longitudinal axis of the throat.

Auricular Muscles

* **Fronto-scutularis** (Figs. 1, 2). This is a small, flat, strap-like muscle found on the dorsolateral surface of the head just posterior to the postorbital process and anterior to the ear.

Origin: Posterior superficial surface of the postorbital process of the frontal and adjacent portion of the parietal crest.

Insertion: Anterior end of the scutiform cartilage.

Relations: Anterior to M. interscutularis and the scutiform cartilage, superficial to M. temporalis.

* **Interscutularis** (Figs. 1, 2). A flat muscle which passes anterolaterally between the parietal crest and scutiform cartilage.

Origin: Posterior parietal crest, nuchal crest and anterior portion of the ligamentum nuchae.

Insertion: On medial and posteromedial border of the scutiform cartilage.

* Denotes muscles which attach either to the cranium or the mandible.

TABLE 1. Geographic distribution of specimens of *Dicotyles tajacu* examined

Geographic area	number	male	female	sex	
				unknown	juvenile
Arizona	7	—	1	5	1
Texas	4	1	—	3	—
Mexico	25	11	7	6	1
Guatemala	1	—	—	1	—
Honduras	3	1	2	—	—
Nicaragua	5	2	2	1	—
Costa Rica	2	—	1	1	—
Panama	1	—	—	1	—
Colombia	40	1	—	29	10
Equador	1	—	1	—	—
Peru	6	2	3	1	—
Venezuela	4	2	2	—	—
British Guiana	7	—	—	7	—
Surinam	1	—	—	1	—
Trinidad	1	—	—	1	—
Brazil	27	8	7	12	—
TOTAL	135	28	26	69	12

Relations: Posterior to the preceding muscle, anterior to M. cervico-scutularis; superficial to M. temporalis.

Cervico-scutularis (Figs. 1, 2). This muscle lies posterior to the preceding, between the nuchal ligament and scutiform cartilage. A slip from the anterolateral portion connects to the anterodorsal corner of the concha.

Origin: From the ligamentum nuchae behind M. interscutularis.

Insertion: On the posterior surface of the scutiform cartilage and on the anterodorsal corner of the concha of the ear, posterodorsal to the insertion of M. scutulo-auricularis superficialis.

Relations: Posterior to M. interscutularis, superficial to M. cervico-auricularis superficialis and parieto-auricularis; medial to concha of ear.

* **Zygomatico-auricularis** (Figs. 1, 2). The presence of this muscle has not been completely demonstrated. It may be represented by a small cylindrical mass which arises from the posterior portion of the zygomatic arch immediately anteroventral to the base of the ear and connects deeply at the anterior base of the conchal cartilage.

Scutulo-auricularis superficialis (Figs. 1, 2). This is a flat triangular muscle lying between the posterolateral surface of the scutiform cartilage and the anterior base of the concha of the ear.

Origin: From the lateral surface of the posterior part of the scutiform cartilage.

Insertion: On the anterior base of the conchal cartilage anterior to the insertion of M. cervico-scutularis.

Relations: Posterolateral to the scutiform cartilage; posterior to M. fronto-scutularis and anterolateral to M. cervico-scutularis.

Parieto-auricularis (Fig. 2). A thin flat muscle which tapers transversely from the nuchal ligament to the posterior portion of the concha.

Origin: From the ligamentum nuchae anterior to and under the cover of M. cervico-scutularis; posterior and above that of M. cervico-auricularis superficialis.

Insertion: On lower surface of convex portion of concha, posterior and ventral to that of M. cervico-auricularis superficialis.

Relations: Deep to M. cervico-scutularis; partly superficial and posterior to M. cervico-auricularis superficialis.

Cervico-auricularis superficialis (Fig. 2). A thin flat muscle, posterior and deep to M. interscutularis, which tapers transversely to attach to the posterior base of the concha.

Origin: On the ligamentum nuchae deep and posterior to the origin of M. interscutularis, anterior to that of M. parieto-auricularis.

Insertion: On the posterodorsal portion of the convex concha anterior and dorsal to that of M. parieto-auricularis.

Relations: Anterior to M. parieto-auricularis, posterior and deep to M. interscutularis, deep to M. cervico-scutularis.

* **Parotido-auricularis** (Figs. 3, 4, 5)¹

A large strap-shaped muscle directed anteroventrally between the base of the ear and the parotid gland.

Origin: Fleshy interdigitation with the parotid gland.

Insertion: A thin sheet along the postzygomatic crest medial to the external auditory meatus, extending up the postzygomatic crest to just below the posterolateral corner of the nuchal crest (Fig. 11).

Relations: Superficial to Mm. cleido-mastoideus, cleido-occipitalis ventralis, serratus ventralis and parotid gland; posterior to M. masseter lateralis, deep to M. cutaneus.

Muscles of the Eyelids

* **Orbicularis oculi** (Fig. 1). This is the only muscle of the eyelid which has been located in this specimen. It is a flat sphincter which encircles the eyelids.

Muscles of the Face

* **Levator nasolabialis** (Fig. 1). A thin flat muscle on the face just under the skin; it is oriented obliquely anteriorly from the rear of the snout to the posterolateral surface of the buttress covering the root of the upper canine.

Origin: On the maxillary and nasal bones dorsal to the anterior end of the facial crest of the maxillary (Fig. 9).

Insertion: On the lips around the canine buttress and forward to the lateral surface of the snout.

Relations: Deep to the skin of the snout; superficial to Mm. dilator naris lateralis, depressor rostri and levator labii superioris proprius.

* **Levator labii superioris proprius** (Fig. 1). A superficial facial muscle which leads anteriorly from the orbital region to the dorsolateral portion of the snout. The anterior portion of the muscle is tendinous.

Origin: A shallow preorbital depression anterior to the fronto-lacrimonal notch of the orbital rim and below the supraorbital canal (Fig. 9).

Insertion: Dorsolateral part of the snout.

Relations: Passes beneath the preceding muscle; lies dorsal to tendon of M. dilator naris lateralis.

* **Dilator naris lateralis** (Fig. 1). A slender muscle which passes anteriorly from the facial crest to the lateral portion of the snout.

Origin: In the anterior part of an ovoid pit on the

¹ The name for this muscle is misspelled Parotoidoauricularis in Figs. 3, 4, and 5.

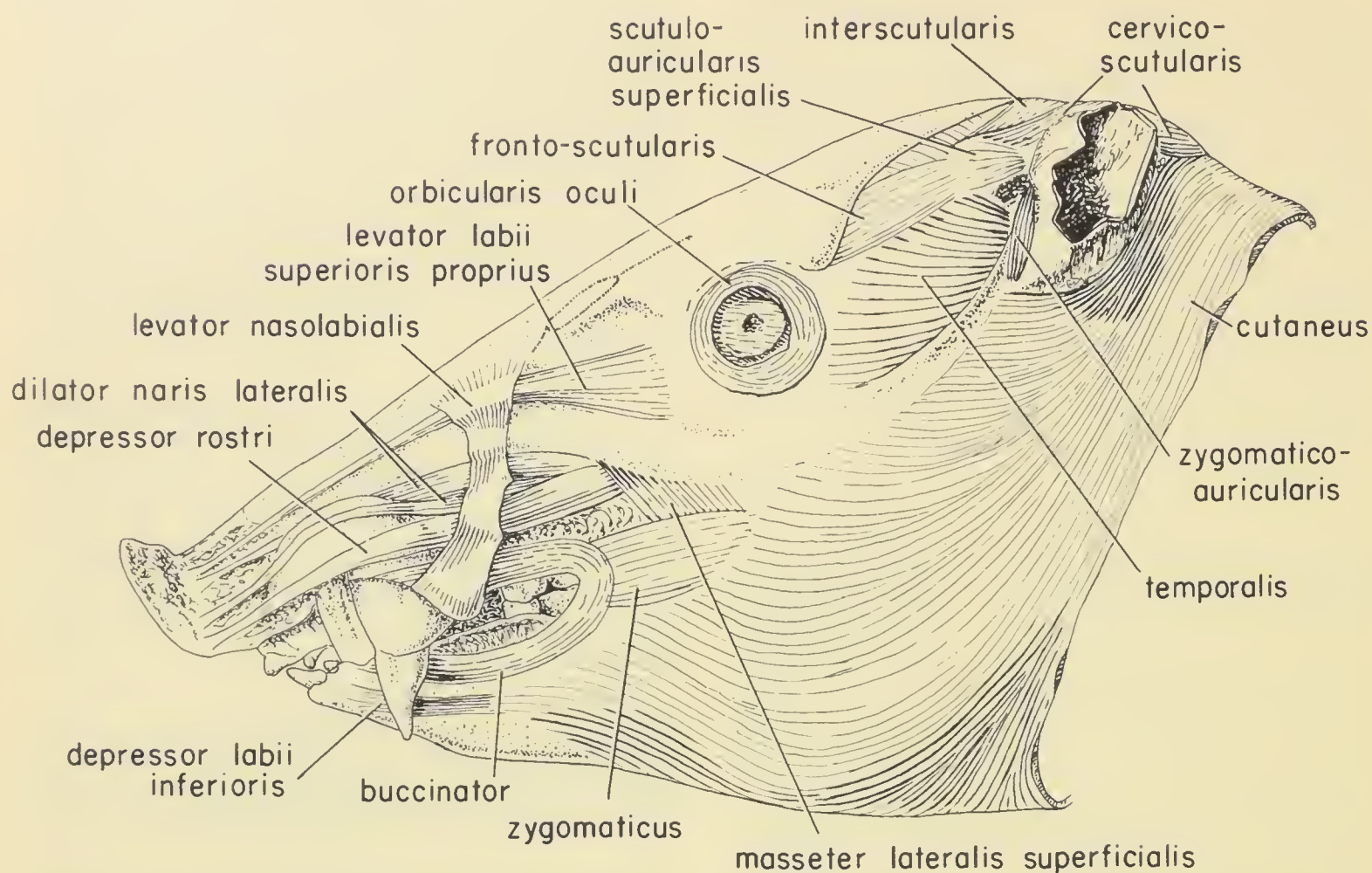


Figure 1. *Dicotyles tajacu*; superficial cranial musculature as seen in left lateral view. About one-half natural size.

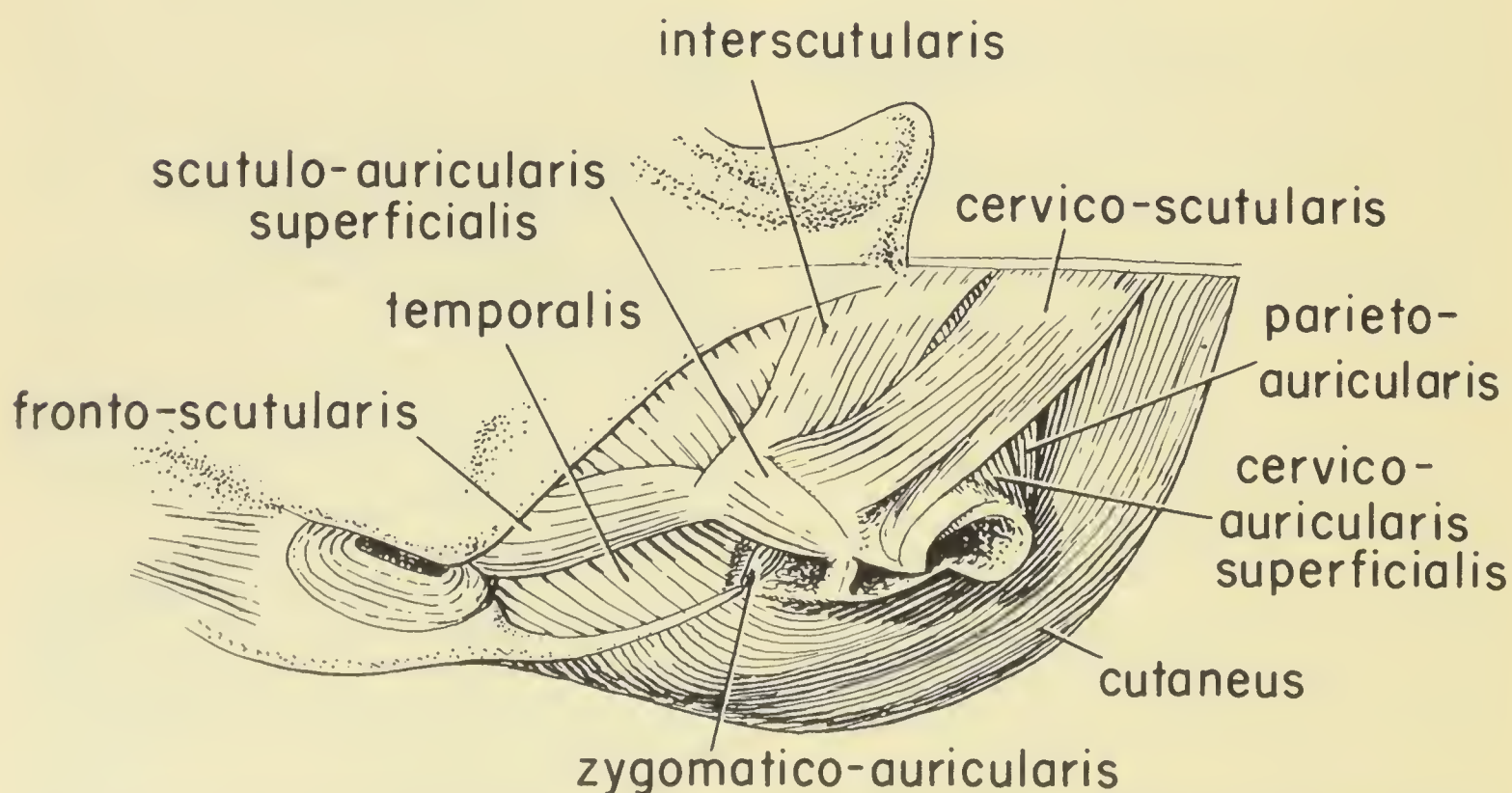


Figure 2. *Dicotyles tajacu*; dorsal aspect of temporal region showing auricular musculature. About three-fourths natural size.

undersurface of the facial crest above M^1 and anterior to a sulcus for the attachment of *M. masseter lateralis profundus* (Figs. 9,10).

Insertion: On lateral part of the snout.

Relations: The muscle splits into two bodies, each of which become tendinous anteriorly. The bodies of the muscle lie dorsal to *M. depressor rostri* and extend anteriorly beneath *M. levator nasolabialis*.

* **Depressor rostri** (Fig. 1). This muscle arises slightly posterior to the preceding, and parallels it to reach the snout. The muscle has also been designated as *M. depressor labii superioris* by various workers.

Origin: The posterior part of the same depression occupied by the origin of the preceding muscle (Fig. 10).

Insertion: Ventrolateral edge of snout.

Relations: Ventral to *M. dilator naris lateralis*, dorsal to *M. buccinator*; passes beneath *M. levator nasolabialis*.

* **Buccinator** (Fig. 1). This muscle forms the lateral wall of the mouth posterior to the canines.

Origin: On and below a strong crest which passes dorsal and parallel to the alveolar border from the rear of the upper canine to a point above M^1 ; then posterodorsally and laterally along the maxillary portion of the base of the zygomatic arch (Fig. 9); in the sulcus at the anterior surface of the coronoid process of the mandible posterior to M_3 and along the lower alveolar border anteriorly to the diastema between the premolar and canine (Fig. 12).

Insertion: Angle of mouth, blending with *M. orbicularis oris*.

Relations: Ventral to body of *M. depressor rostri*, deep to *M. masseter medialis posteriorly* and *M. zygomaticus*; dorsal to and posteriorly interfingering with *M. depressor labii inferioris*.

Zygomaticus (Fig. 1). A short, flat superficial muscle between the anterior edge of *M. masseter lateralis superficialis* and *M. buccinator*.

Origin: In fascia of anterior surface of *M. masseter lateralis superficialis* and *M. cutaneus*.

Insertion: Fascia of the midlateral portion of *M. buccinator* near the angle of the mouth.

Relations: Ventral to *M. depressor rostri*, deep to *M. levator nasolabialis*; anterior to *Mm. cutaneus* and *masseter lateralis superficialis*.

* **Depressor labii inferioris** (Figs. 1, 5). A long thin largely tendinous muscle which extends antero-ventrally from the anteromedial surface of the coronoid process of the mandible to the ventrolateral lips.

Origin: In common with *M. buccinator* along the posterior alveolar border of the mandible and medial surface of the coronoid process (Figs. 12,13).

Insertion: In the tissue of the lips at the ventrolateral tip of the mouth anterior to the canines.

Relations: Ventral to *M. buccinator*.

Muscles of the Neck and Adjacent Cranium
Brachiocephalicus. The muscle occupies the dorsal and lateral aspect of the neck and occipital area deep to *M. cutaneus*; it is divided into two major parts in the peccary. *M. cleido-occipitalis*, dorsal of the two divisions, is also divisible into two parts on the basis of their origins; the *Mm. cleido-occipitalis dorsalis* and *ventralis*. The insertions for these muscles, and for *Mm. rhomboideus* and *splenius*, were not determined during this dissection as the animal's head had been separated from its body.

Cleido-occipitalis dorsalis (Fig. 3)

Origin: As a flat sheet on the nuchal ligament posterior and deep to *M. interscutularis*.

Relations: Superficial to *Mm. rhomboideus*, *splenius* and *serratus ventralis*; posterior to *M. parotido-auricularis*.

Cleido-occipitalis ventralis (Figs. 3-6).

Origin: On the mid-anteroventral wing of the atlas.

Relations: Ventral to *M. splenius mastoideus* and *serratus ventralis* and dorsal to *M. cleido-mastoideus*.

* **Cleido-mastoideus** (Figs. 3-6, 10). This distinct muscle, which lies posterior and deep to the parotid gland, is the second major division of *M. brachiocephalicus*.

Origin: Just ventral to that of *M. splenius mastoideus* (Figs. 15,16).

Relations: Anteroventral to *Mm. cleido-occipitalis ventralis* and *splenius mastoideus*; deep to the parotid gland; dorsal to *M. sternomastoideus*.

Rhomboideus (Figs. 3, 4). This is a relatively small, thin, flat muscle with two points of origin which occupies the dorsomedial portion of the neck near the nuchal ligament. The two heads have received the following designations:

Rhomboideus cervicalis (Fig. 5). *Origin:* Along the nuchal ligament, but not quite reaching the occiput of the cranium. The muscle passes posterolaterally to join the fibers of the second part.

* **Rhomboideus capitis** (Fig. 5). *Origin:* As a thin slip for about $\frac{1}{2}$ " along the postzygomatic crest just below the posterolateral corner of the nuchal crest. The site of origin is deep to that of *M. parotido-auricularis* (Fig. 11).

Relations: The two slips merge posterolaterally and are deep to *M. cleido-occipitalis dorsalis*, superficial to *M. splenius mastoideus* and are bound by fascia to the small dorsal slip of *M. serratus ventralis*.

Splenius (Figs. 3, 4). An extensive muscle on the dorsal and lateral surface of the neck, the fibers of which are directed anterolaterally. The muscle is undivided posteriorly but separates into two distinct heads anteriorly, *M. splenius capitis* and *M. splenius mastoideus*. The mastoid portion is in turn separated into a dorsal, mastoid, portion and a ventral portion, *M. splenius cervicis*.

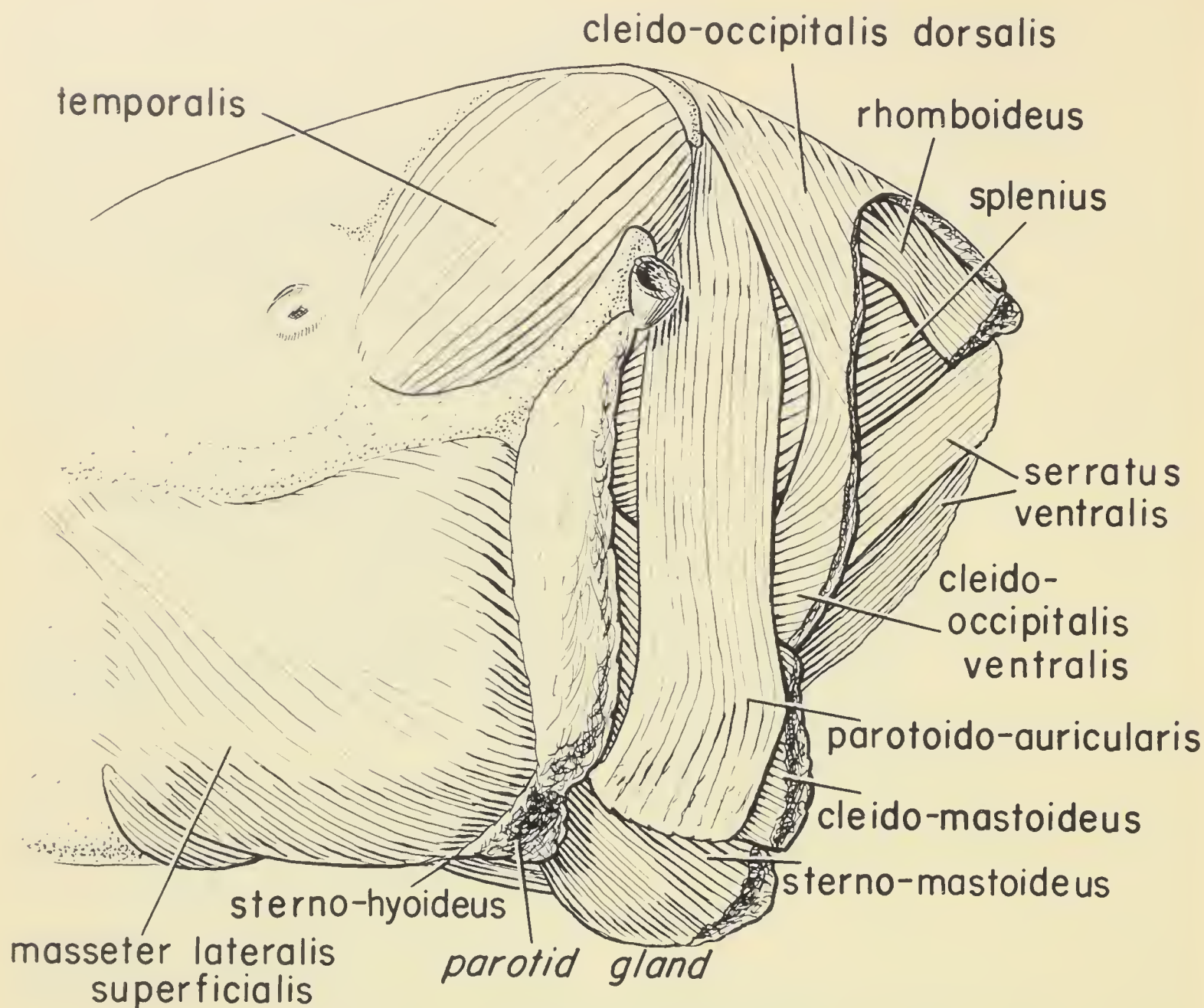


Figure 3. *Dicotyles tajacu*; superficial musculature of posterior portion of the cranium after removal of M. cutaneus. About three-fifths natural size.

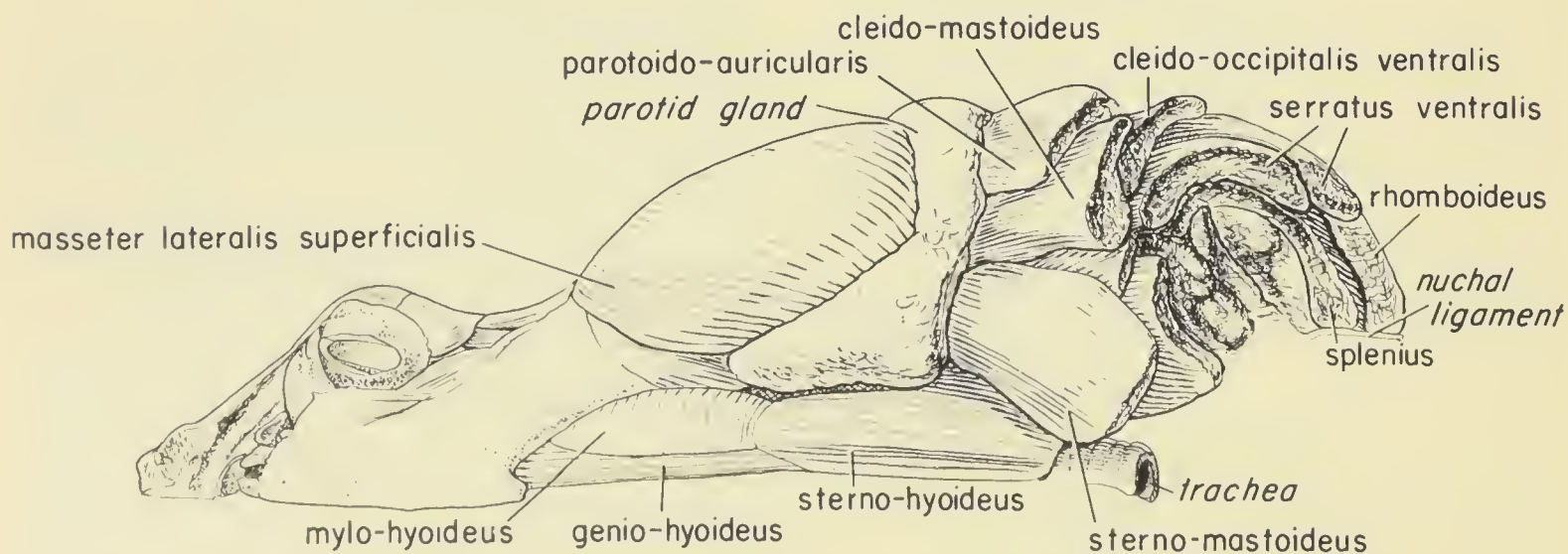


Figure 4. *Dicotyles tajacu*; ventral view of head showing superficial muscles after the removal of M. cutaneus. About one-half natural size.

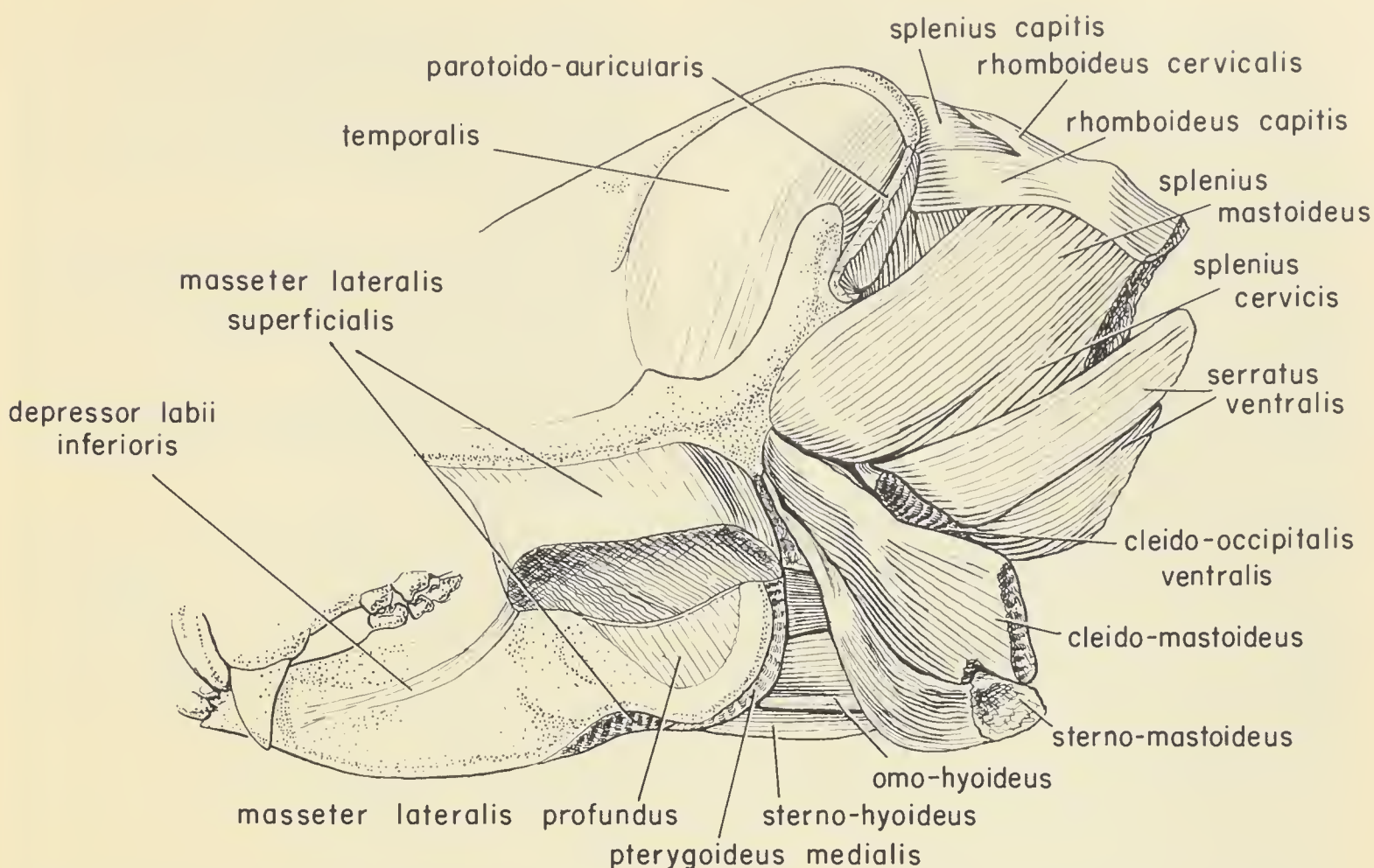


Figure 5. *Dicotyles tajacu*; slightly deeper dissection of the left lateral aspect of the head. About one-half natural size.

* **Splenius capitis** (Fig. 5): The insertion is on the upper half of the rugose rim of the occiput below and parallel to the nuchal crest (Fig. 11).

* **Splenius mastoideus** (Fig. 5): This branch inserts on the mastoid region of the zygomatic arch below the external auditory meatus and dorsal to the postglenoid process (Figs. 10, 11).

Splenius cervicis (Figs. 5, 6): The insertion is on the tip of the wing of the atlas.

Serratus ventralis (Figs. 3-6). This muscle mass consists of two parts, the dorsal part being more slender than the ventral. These probably correspond to the M. serratus cervicis branch of the serratus group and thus originate farther forward than in the horse, but about the same as in the ox and pig (see Sisson and Grossman, 1953, pp. 299, 353, 364).

Another possible interpretation is that the dorsal part corresponds to M. serratus cervicis while the larger, ventral, part corresponds to M. serratus thoracis which would, in this case, attach quite high on the neck.

Origin: Dorsal part: along the anteroventral surface of the tip of the atlantal wing. Ventral part: along the ventral surface of the transverse process of the axis and cervical vertebrae 3-5; deep surface of the posterior corner of the atlantal wing.

Relations: Ventral to Mm. splenius mastoideus and splenius cervicis; deep to M. cleido-occipitalis ventralis; superficial to M. semispinalis capitis.

* **Semispinalis capitis** (Fig. 6). This muscle forms a deep segment of the neck musculature and attaches to a correspondingly deep part of the occiput. In other animals, two muscle masses, a dorsal M. biventer cervicis and a ventrolateral M. complexus or M. complexus major may be differentiated.

In the collared peccary the two divisions are not readily distinguishable. The fibers form a relatively thin sheet, the bundles of which are directed posterolaterally from the nuchal crest.

Insertion: On the nuchal crest below M. splenius capitis from midline to posterolateral corner of nuchal crest (Fig. 11).

Relations: Superficial to Mm. obliquus capitis anterior and obliquus capitis posterior, rectus capitis dorsalis major and minor; deep to Mm. rhomboideus, splenius and longissimus capitis.

* **Sterno-mastoideus** (Figs. 3-5). A massive muscle between Mm. cleido-mastoideus and masseter lateralis superficialis. The muscle tapers markedly toward its tendinous insertion on the mastoid area just dorsal to the postglenoid process on the crest which curves dorsolaterally from that process toward the base of

the external auditory meatus. The insertion area is bounded dorsally, laterally and ventrally by that of *M. cleidomastoideus* (Figs. 10, 11).

Relations: Inserted between *Mm. cleidomastoideus* and *M. masseter lateralis superficialis*; superficial to *M. omo-hyoideus*; deep to parotid gland and *M. parotido-auricularis*.

* **Longissimus capitis et atlantis** (Fig. 6). This muscle is composed of a dorsal (*capitis*) and ventral (*atlantis*) portion. The dorsal slip is much more massive than the ventral. Both lie deep to *Mm. splenius mastoideus* and *splenius cervicis*.

Insertion: Dorsal portion: On the mastoid region of the cranium below the external auditory meatus deep to the dorsal half of the insertion of *M. splenius mastoideus* (Fig. 11). Ventral portion: On the posterior surface of the wing of the atlas.

Relations: Deep to *Mm. splenius mastoideus* and *splenius cervicis*; superficial to *Mm. semispinalis capitis* and *obliquus capitis anterior*.

* **Obliquus capitis anterior** (Figs. 6, 7). This muscle arises from the anterior and dorsal surface of the wing of the atlas and apparently divides into two heads; one extends vertically, the other anteriorly.

Origin: On the anterior and dorsal surface of the wing of the atlas.

Insertion: (1) the dorsal head inserts on the postzygomatic crest below the posterolateral corner of the nuchal crest; the insertion area lies deep to but parallels that for the origin of *M. parotido-auricularis* (Fig. 11). (2) The more ventral head inserts on the mastoid area ventral to the external auditory meatus, deep to the insertions of *Mm. longissimus capitis*, *splenius mastoideus*, *sterno-mastoideus* and *cleidomastoideus*. The insertion area of ventral head of *M. obliquus capitis anterior* extends medially to the squamosooccipital suture and ventrally to the dorsolateral base of the paroccipital process (Figs. 10, 11).

Relations: Superficial to *Mm. rectus capitis dorsalis major* and *minor* and *M. rectus capitis lateralis*; deep to the muscles listed above.

Obliquus capitis posterior (Fig. 7). This horizontally oriented muscle lies between the dorsal surface of the axis and the posterior dorsal surface of the atlas.

Origin: On the spine and lateral surface of the transverse process of the axis.

Insertion: On the posterior dorsal surface of the wing of the atlas.

Relations: Dorsal to all but the spine of the axis; ventral to *M. rectus capitis dorsalis minor*; deep to *M. semispinalis capitis*.

* **Rectus capitis dorsalis major** (Fig. 7). A thick muscle which extends from the axis to the occiput in contact with the nuchal ligament. This is one of the deepest muscles of the occiput.

Origin: Along the dorsal spine of the axis.

Insertion: On nearly all of the occipital surface deep and medial to the attachment areas of the other occipital muscles. The muscle extends down along the upper fourth of the foramen magnum, then dorsally medial and parallel to the postzygomatic crest (Fig. 11).

Relations: This is the deepest muscle of the dorsal neck region. At its lower lateral corner, it is covered by *M. rectus capitis dorsalis minor*; it is overlain dorsally and laterally by *M. semispinalis capitis*.

* **Rectus capitis dorsalis minor** (Fig. 7). A smaller muscle lateral and ventral to the above.

Origin: On the lateral surface of the spine of the axis.

Insertion: On the medial surface of the postzygomatic crest between the insertion of preceding and that of *M. obliquus capitis anterior* (Fig. 11).

Relations: Deep to *M. obliquus capitis anterior*; lateral to *M. rectus capitis dorsalis major*.

* **Rectus capitis lateralis**. A short muscle which lies between the median anterior surface of the atlas and the base of the paroccipital process.

Origin: On the medial half of the anterior surface of the wing of the atlas.

Insertion: Along the posterior surface and base of the paroccipital process and the posterior and ventral surface of the condyloid sulcus (Fig. 10).

Relations: Lateral to *M. rectus capitis ventralis minor*; deep to *M. obliquus anterior* (ventral portion); anteromedial to *M. obliquus capitis anterior*.

* **Rectus capitis ventralis major** (Figs. 7, 8). An elongate muscle applied to the ventral aspect of the cervical vertebrae and basilar region of cranium; the muscle divides into two slips posteriorly.

Origin: On the ventral surface of transverse processes of cervical vertebrae 3 and 4.

Insertion: Along the basisphenoid and basioccipital bones of the cranium, medial and slightly anteromedial to the edge of the bulla (Fig. 10).

Relations: Deep to *Mm. cleido-mastoideus* and *sterno-mastoideus*; ventral to *M. serratus ventralis*; dorsal to *Mm. sterno-thyroideus*, *thyro-hyoideus*, *ventricularis*; ventral to *M. rectus capitis ventralis minor*.

* **Rectus capitis ventralis minor**. This is a slender muscle lying dorsal and slightly posterior to the preceding.

Origin: On the ventral arch of the atlas.

Insertion: This is not clearly differentiated from that of *M. rectus capitis lateralis posteriorly*. The insertion area lies along the ventral surface of the basioccipital, medial to the bulla and anteriorly nearly to the basioccipito-basisphenoid suture (Fig. 10).

Relations: Posterior and dorsal to insertion of *M.*

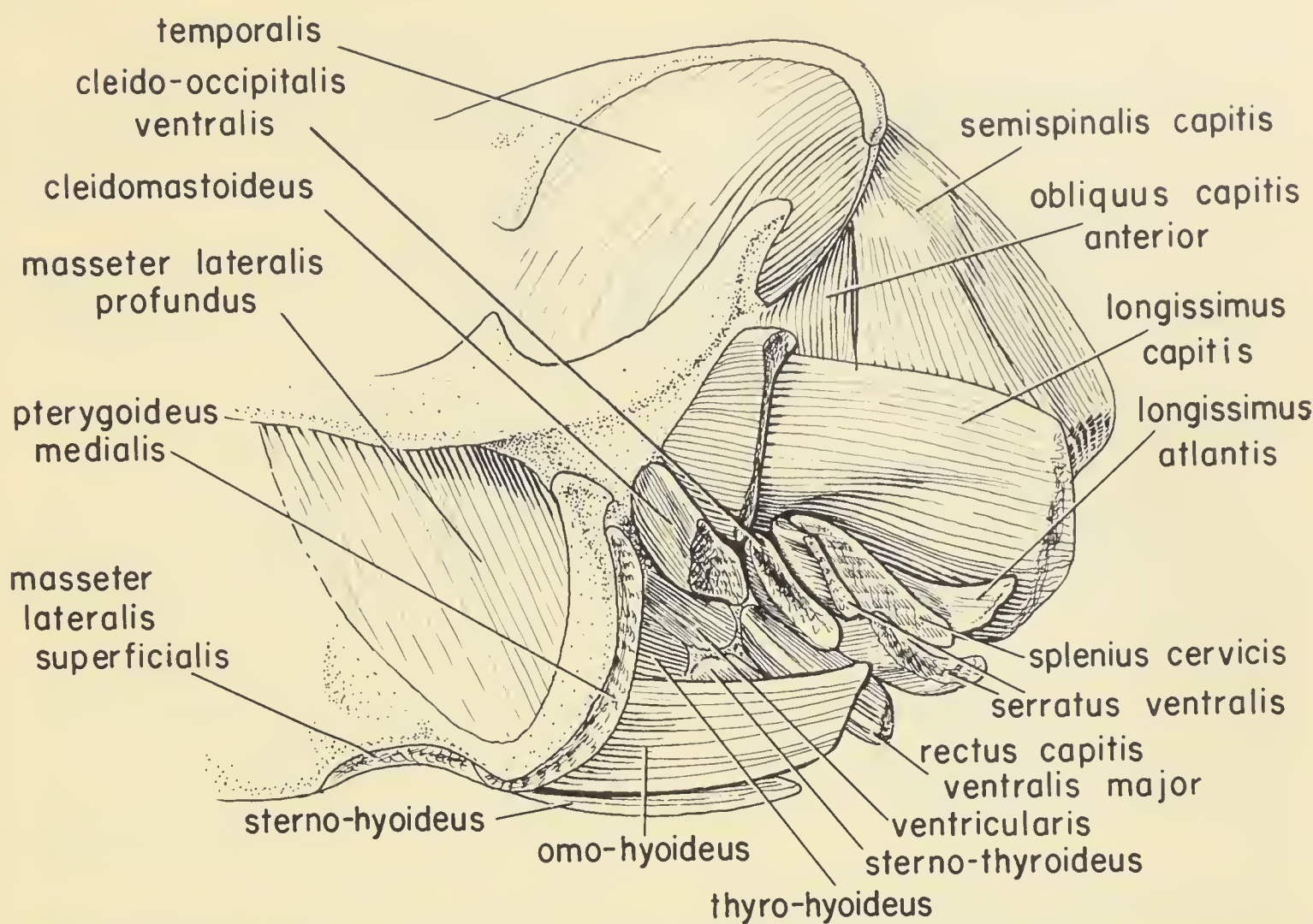


Figure 6. *Dicotyles tajacu*; left lateral view of the posterior portion of the head showing some of the deeper muscles of the throat and neck. Slightly larger than one-half natural size.

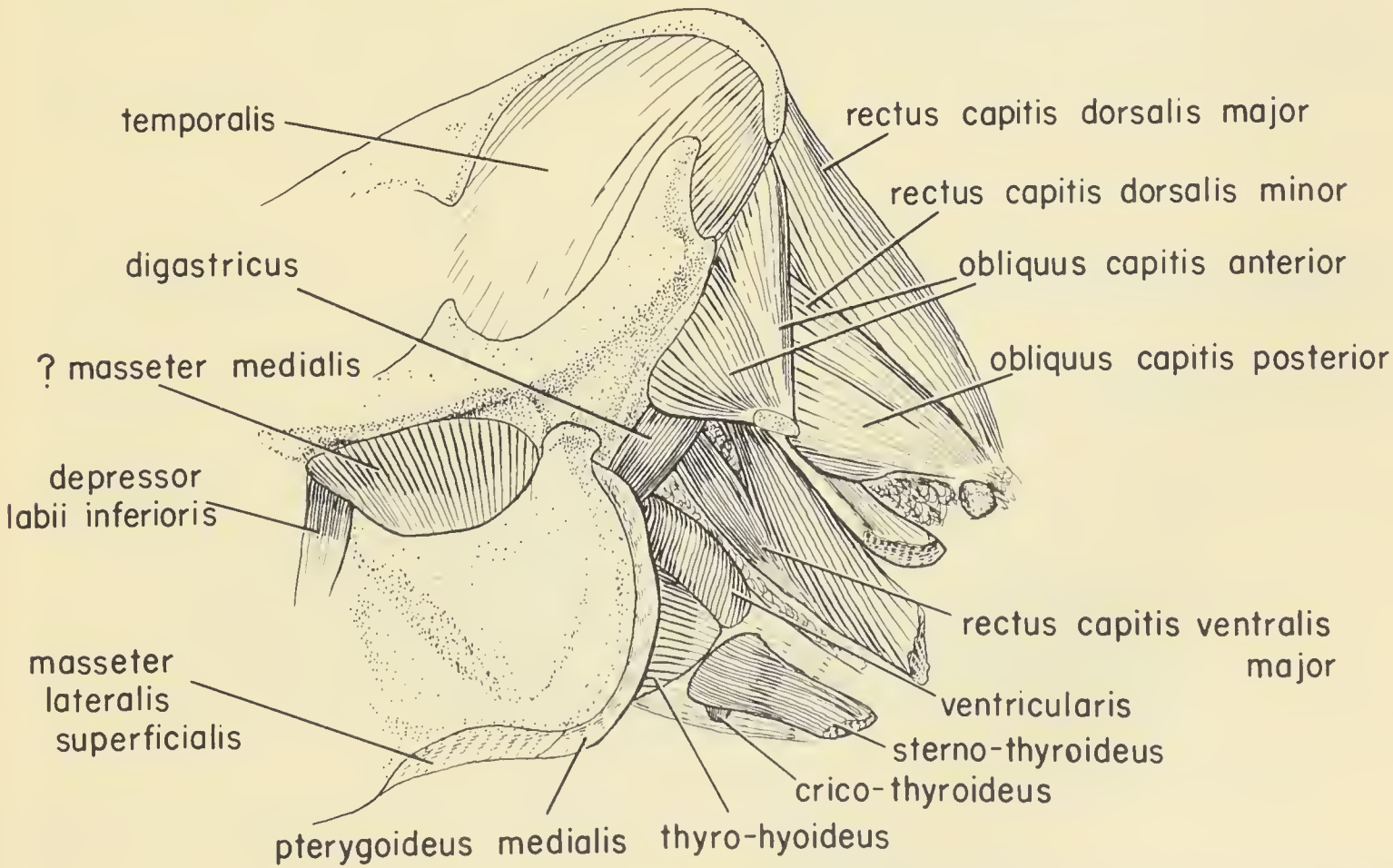


Figure 7. *Dicotyles tajacu*; left lateral view of the posterior portion of the head showing mainly the deep musculature of the throat and neck. About one-half natural size.

rectus capitis ventralis major medial to M. rectus capitis lateralis.

Ventral cervical and hyoid musculature

* **Mylo-hyoideus** (Figs. 4, 8). A flat sheet covering the ventral aspect of the throat anterior to M. sterno-hyoideus.

Origin: From the medial surface of the mandible at the rear of the symphysis, continuing posterodorsally along a slightly roughened line to a point just below the rear of the last molar (Fig. 13).

Insertion: On a median raphe from the symphysis to the hyoid bone anterior to Mm. sterno-hyoideus and omo-hyoideus.

Relations: Deep to Mm. cutaneus; anterior to Mm. sterno-hyoideus and omo-hyoideus; superficial to M. genio-hyoideus.

* **Genio-hyoideus** (Fig. 4). A long slender muscle which extends longitudinally between the symphysis and hyoid bone.

Origin: In the genial pit just posterior to the symphysis on the medial surface of the mandible in common with the origin of Mm. genio-glossus and the anterior tip of mylo-hyoideus. (Fig. 13).

Insertion: On the lingual process of the hyoid bone.

Relations: Deep to Mm. mylo-hyoideus and thyro-hyoideus; superficial to M. crico-thyroideus.

* **Genio-glossus** (Fig. 8). A fan-shaped muscle between the symphysis and the base of the tongue.

Origin: On the medial surface of the mandible in common with the Mm. genio-hyoideus and mylo-hyoideus (Fig. 13).

Insertion: Fibers fan out from the origin to insert posterodorsally in the base of the tongue.

Relations: Deep to M. genio-hyoideus

The following muscles could be differentiated in the peccary but are not treated further as they make no important connections to the cranium. Several have been figured.

Omo-hyoideus; sterno-hyoideus; * stylo-hyoideus; thyro-hyoideus; hyo-glossus; crico-thyroideus; * stylo-glossus; * palatinus; * levator palati; * tensor palati; * occipito-hyoideus.

Mandibular Muscles

Masseter lateralis. This muscle is divided by a sheet of fascia into superficialis and profundus portions. * Masseter lateralis superficialis (Figs. 3-7). This muscle forms the bulk of M. masseter as seen in lateral aspect.

Origin: Thinly along the zygomatic arch, generally in association with a sharp crest, posterodorsal to the glenoid fossa; then anteriorly to a point above M¹ (Figs. 9,10).

Insertion: On the border of mandible from the base of the condyle to the anterior end of the post-digastric sulcus. On the ventral border, this muscle extends across that sulcus to the medial surface, blending to a slight degree with M. pterygoideus medialis (Figs. 12,13).

Relations: Deep to M. cutaneus, superficial to M. masseter lateralis profundus.

* **Masseter lateralis profundus** (Figs. 5, 6). *Origin:*

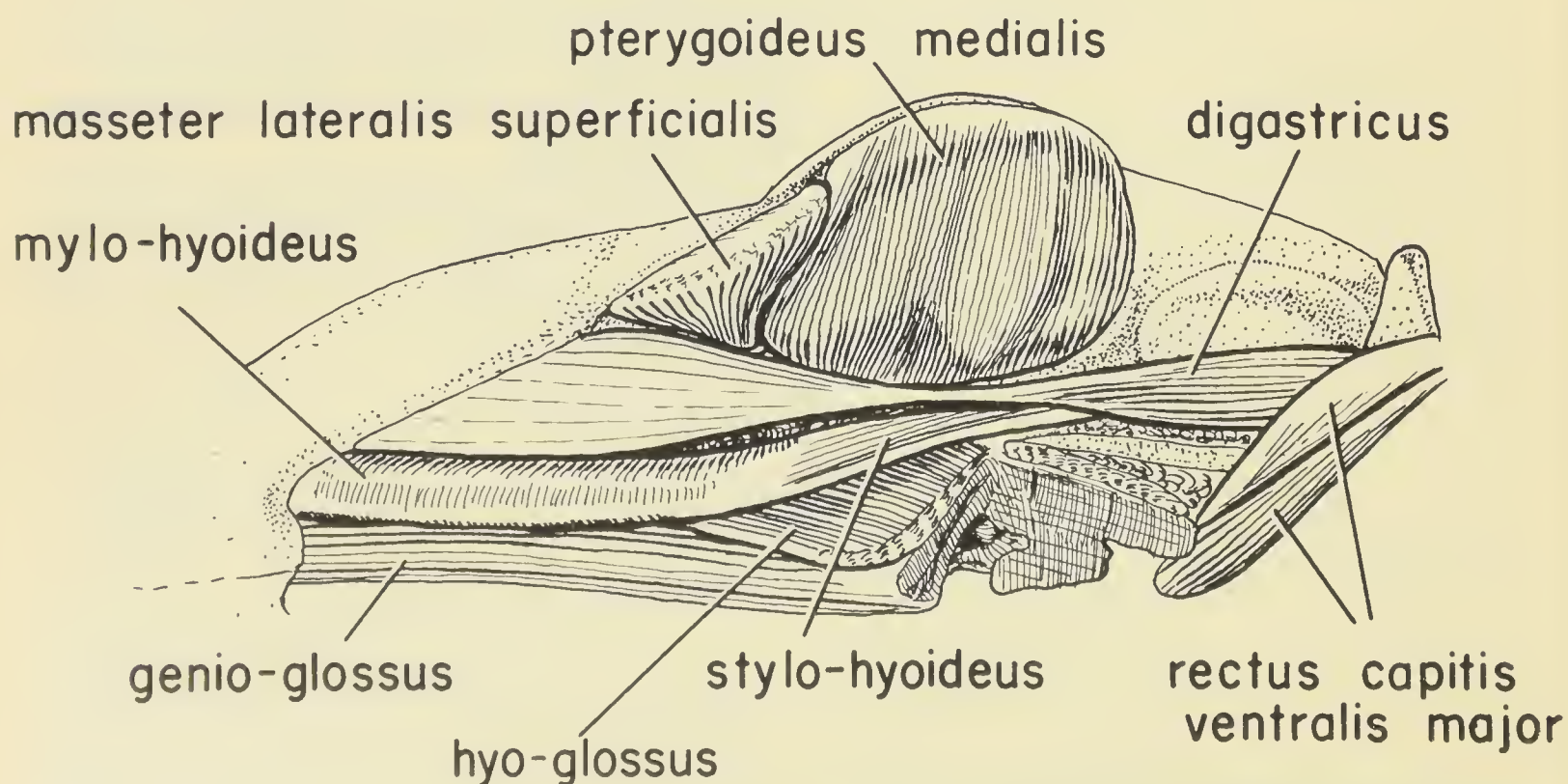


Figure 8. *Dicotyles tajacu*; deep ventral musculature of the throat and neck. About three-fourths natural size.

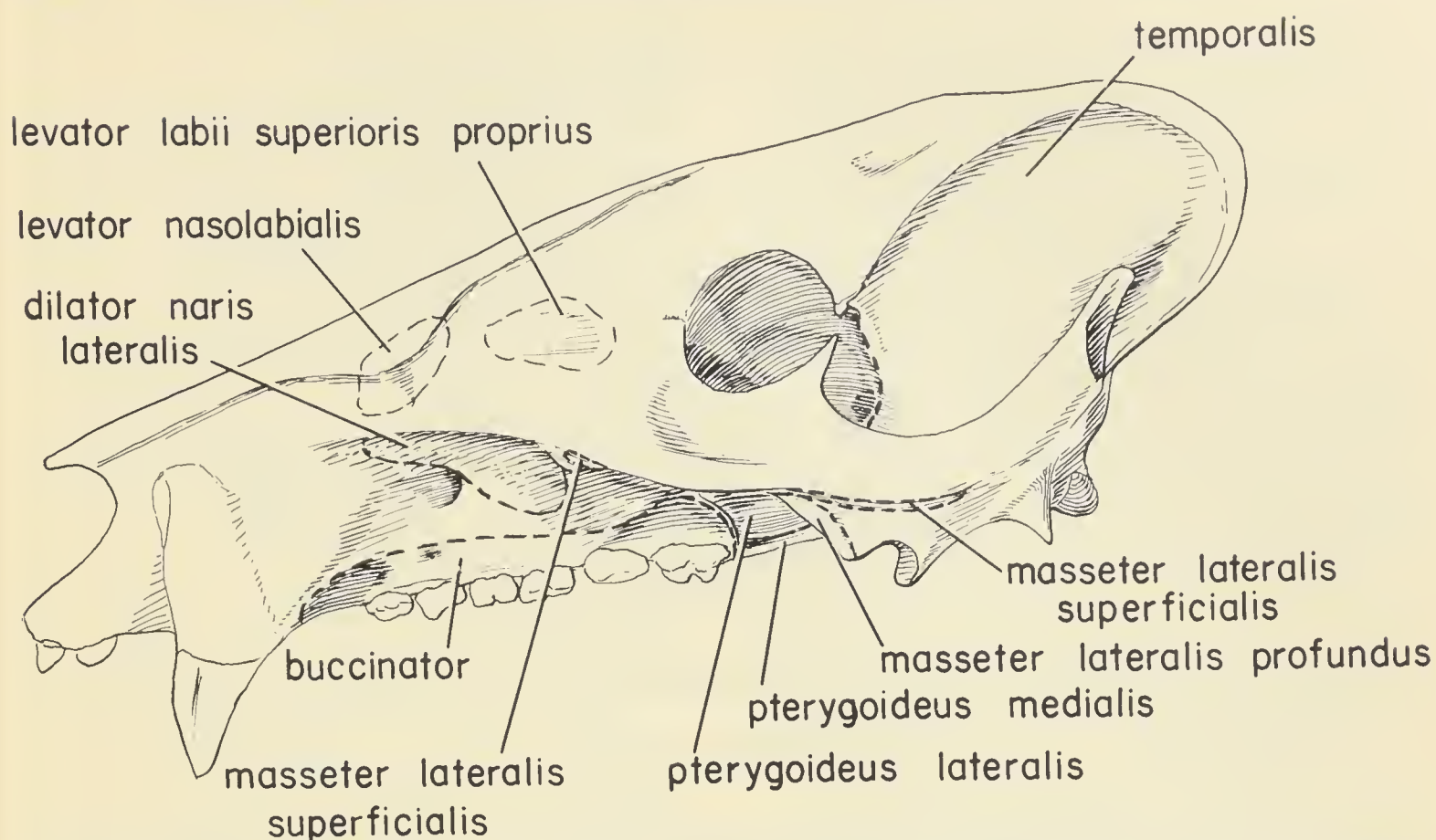


Figure 9. *Dicotyles tajacu*; left lateral view of the cranium showing the attachment areas of the major muscles. About one-half natural size.

Deep to the preceding, on the ventral surface of the zygomatic arch medial to the crest of the arch (Fig. 10).

Insertion: In the masseteric fossa of the mandible (Fig. 12).

Relations: Deep to M. masseter lateralis superficialis; deep to M. ?masseter medialis; posterior to Mm. dilator naris lateralis; depressor rostri and depressor labii inferioris.

* **?Masseter medialis** (Fig. 7). This muscle may be present, although poorly differentiated from the lateral portion of M. temporalis.

Origin: Along the medial edge of the ventral portion of the zygomatic arch.

Insertion: In the coronoid fossa on the lateral surface of the mandible. (Fig. 12).

Relations: Ventral to the main body of M. temporalis; deep to M. masseter lateralis profundus.

* **Temporalis** (Figs. 1-3, 5-7). This large muscle occupies the temporal fossa of the cranium, passes medial to the zygomatic arch and inserts on the coronoid process of the mandible.

Origin: From the postorbital process of the frontal posteriorly along the parietal crest; the anterior edge of the nuchal and postzygomatic crests; the anterior surface of the bony covering of the external auditory meatus; anteriorly along the dorsal edge of the medial surface of the zygoma to the postorbital process of the jugal; from this the line of origin

continues anteroventrally, following the curve of the maxilla to the maxillary tuberosity above M^3 , then posteriorly along the ventral edge of the zygoma to the glenoid fossa; thence along the squamosal to the anterodorsal edge of the bulla medially to the infratemporal crest and dorsally to the base of the postorbital process of the frontal (Fig. 9).

Insertion: On the dorsal tip of the coroid process by a strong tendon (Figs. 12,13).

Relations: This is the major muscle in the temporal fossa; medial to M. ?masseter medialis ventrally.

* **Digastricus** (Figs. 7, 8). A long thin double bellied muscle situated obliquely between the paroccipital process and the anterior medial surface of the mandible.

Origin: Along the ventromedial border of the paroccipital process superficial to M. stylo-hyoideus (Fig. 10).

Insertion: On the medial surface of the mandible just posterior to the symphysis, dorsal to the ventral border of the mandible (Fig. 13).

Relations: The muscle passes deep to M. pterygoideus medialis as a tendon; lateral to M. mylo-hyoideus; superficial to Mm. genio-hyoideus, hyoglossus, stylo-glossus and stylo-hyoideus.

* **?Occipito-mandibularis**

This muscle apparently lies between the paroccipital process and the posterior edge of the mandible. It is poorly differentiated from M. digastricus.

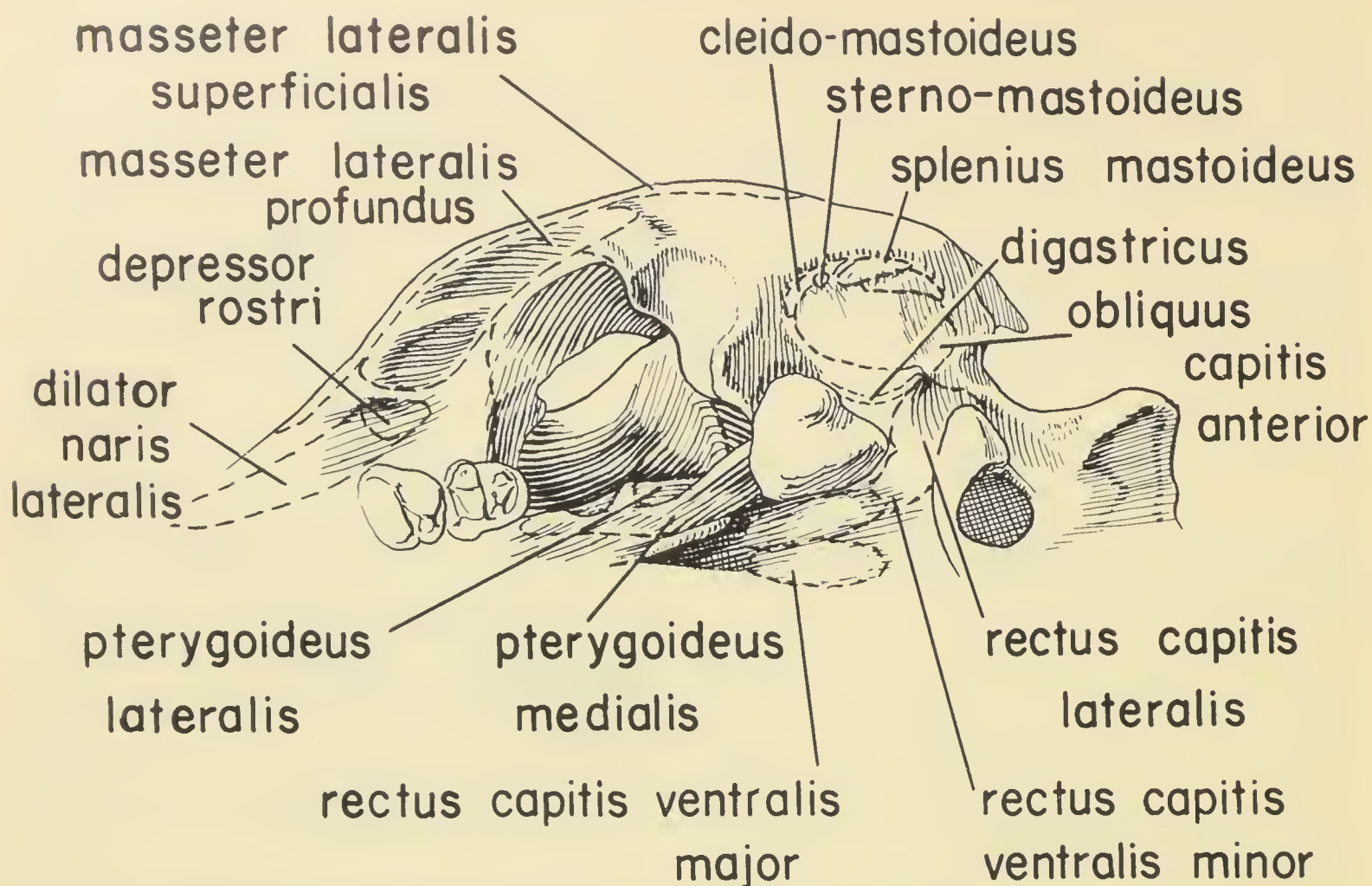


Figure 10. *Dicotyles tajacu*; ventral view of left half of the posterior portion of the cranium showing the attachment areas of the major muscles. About three-fourths natural size.

***Pterygoideus medialis** (Figs. 5-8). This muscle is the counterpart of *M. masseter lateralis superficialis* on the medial surface of the mandible.

Origin: Along the ventral surface of the alisphenoid in the pterygoid fossa, lateral to the hamular process of the pterygoid bone (Figs. 9,10).

Insertion: From the medial edge of the coronoid process of the mandible opposite the rear of M_3 , down the anterior end of the angle of the mandible, along the ventral surface of the angle and posterior side of a dorsally projecting spine, then up to the ventral edge of the condyle (Fig. 13).

Relations: The area of insertion is thin, forming a band peripheral to that of *M. pterygoideus lateralis* on the medial surface of the mandible.

* **Pterygoideus lateralis**. *Origin*: The lateral edge of the ventral surface of the alisphenoid dorsally into the pterygopalatine fossa and anteriorly to a point above M^3 (Figs. 9,10).

Insertion: On the medial surface of the mandible central to the area circumscribed by the insertion of the preceding (Fig. 13).

Relations: This muscle forms the bulk of the pterygoid musculature.

Variation in Muscle Scars

It is often tempting to reconstruct the musculature of

an extinct animal from its fossilized hard parts. A number of observations made during this study may serve to encourage caution in such exercises. One hundred thirty-five specimens of *Dicotyles tajacu* in the collections of the Department of Mammalogy, the American Museum of Natural History, were examined with regard to individual variation. Although minor variations in cranial osteology could be found, marked departures from the general morphologic plan of *Dicotyles* were not observed, even though geographic range of the collection is wide (Table 1). In general, specimens from Colombia seemed to be somewhat smaller and more lightly constructed, and had less well defined attachment areas for such muscles as *M. digastricus* and *M. mylo-hyoideus* than was the case for specimens from other areas. Moreover, one-fourth of the Colombian specimens were juvenile (deciduous premolars still functional). Considering the collection as a whole, minor variations in the configuration of the cranium include the degree of anterior tapering of the rostrum as seen from above, the strength of the facial crest, the development and posterior extent of the crest marking the dorsal limit of *M. buccinator* in the diastemal region, the degree of roundness of the cross section of the infraorbital foramen, the strength of the canine buttresses, the depth of the concavity

developed on the dorsolateral surface of the zygomatic arch below the orbit and the relative breadth of the cranium across the zygomatic arches at the postglenoid processes. In the mandible, the strength of the attachment area for *M. temporalis*, the degree of rugosity in the masseteric and pterygoid fossae, the depth of the digastric fossa, the relative size of the postdigastric sulcus and the degree of rugosity of the origin of *M. mylo-hyoideus* are the major features, related to muscle attachments, in which variation was noted.

Of the 47 muscles described in the preceding section 36 attach either to the cranium or to the mandible. Of these, only 11 are associated with sufficiently distinctive structures that their areas of attachment may be readily determined. In most cases, these structures are such integral features of the cranium as to be essentially immune to significant individual variation. The areas of attachment for the 11 muscles in question are as follows:

1. *M. temporalis*: The temporal fossa in which this muscle originates is clearly defined in all cases. Even at its anterior end, the temporal fossa is separated by a slight vertical ridge (infratemporal crest) from the orbital and pterygopalatine fossae.

M. temporalis inserts on the dorsal tip of the coronoid process of the mandible (Figs. 12, 13). This structure was easily discernible in all cases although the ventral limit of the muscle on the lateral surface of the mandible is not determinable on the bone. The cavity on the coronoid process which lies dorsal to the masseteric fossa and which is often known as the temporal fossa of the mandible may house *M. masseter medialis* in the peccary.

2. *M. masseter lateralis superficialis*: The site of origin of this muscle, taken as the edge of the sharp, ventrally directed crest at the ventrolateral edge of the zygomatic arch, is distinctly marked in all specimens examined. As indicated in Figure 9, a few fibers of this muscle attach above and posterior to the glenoid fossa, but this site of attachment was not well marked on any of the crania examined.

The insertion of *M. masseter lateralis superficialis* was clearly visible only in the dissected specimen. A few of the specimens in the American Museum approached, but did not equal, this degree of rugosity.

3. *M. masseter lateralis profundus*: The muscle originates in an elongate, relatively deep, ventrally facing concavity located on the ventral edge of the zygomatic arch just medial to the origin of the preceding muscle. The origin of *M. masseter lateralis profundus* was easily determinable in all specimens examined although in no case was its site of insertion separable from that for *M. masseter lateralis superficialis*.

4. *M. buccinator*: This muscle originates, on the cranium, in an elongate, laterally facing, concavity. This concavity or fossa, as it might be termed when well developed, lies just dorsal to the alveolar border from the base of the canine to the level of M^1 or M^2 . In some specimens, the crest which defines the dorsal edge of the fossa reaches only to the last premolar. In no instance was the posterior limit of the origin of *M. buccinator*, i.e., above the last molar on the underside of the maxillary base of the zygomatic arch, clearly indicated. The site of origin of this muscle on the mandible was never found to be indicated in any way.

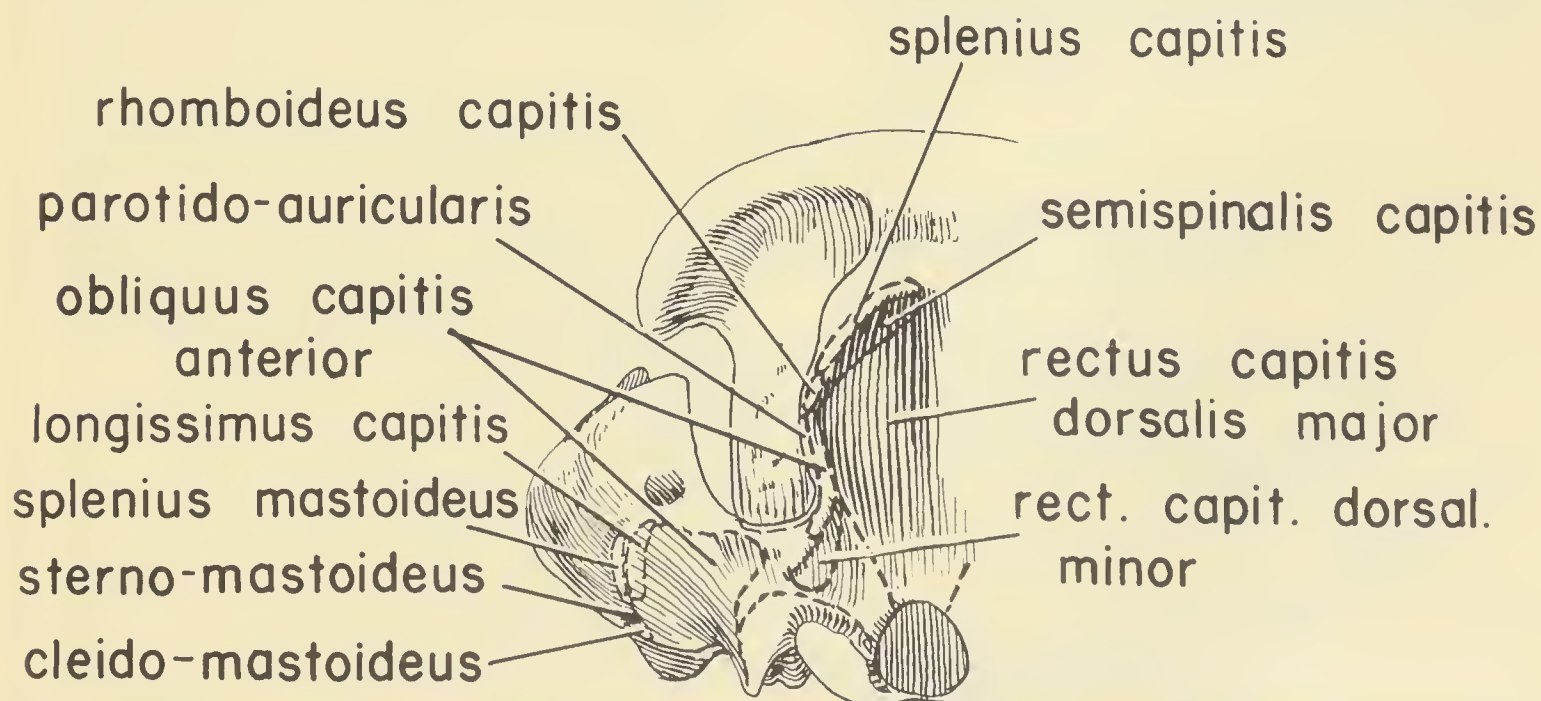


Figure 11. *Dicotyles tajacu*; posterior view of left half of the occiput showing the attachment areas of the major muscles. About three-fourths natural size.

5. *M. rectus capitis dorsalis major*: This muscle inserts in the occipital fossa (Fig. 11) which was found to be well developed in all except the most immature crania (those with none but deciduous teeth). The ventral and ventrolateral limits of the insertion of this muscle were never well defined.

6. *M. rectus capitis dorsalis minor*: This muscle inserts on a tear-drop shaped area above the base of the paroccipital process. A thin, distally tapering process is occasionally developed at the lateral edge of this insertion area. Of the 135 specimens examined the configuration of the insertion of *M. rectus capitis dorsalis minor* could be adequately determined on only 34 crania. Twelve of these crania were of male individuals, 5 were female and in 17 the sex was not determined.

7. *M. pterygoideus medialis*: The site of origin occurs on the lateral surface of the hamular process of the pterygoid and adjacent ventral surface of the alisphenoid, reaching posteriorly along that surface to the anteromedial corner of the bulla. In the sense that this flat ventral strut of alisphenoid and associated pterygoid are always well defined, the origin of *M. pterygoideus medialis* is always visible in the peccary.

8. *M. pterygoideus lateralis*: The muscle originates roughly from the pterygopalatine fossa, the dorsal limit of which corresponds to a strong ridge which extends posteriorly from the roof of the sphenopalatine foramen toward the optic foramen. Inasmuch as the pterygopalatine fossa is usually well defined in *Dicotyles* the area of origin for *M. pterygoideus lateralis* is also determinable.

As mentioned above, the site of insertion of the muscle could not be distinguished from that of *M. pterygoideus medialis* in any of the crania in the American Museum of Natural History.

9. *M. rectus capitis ventralis major*: This muscle inserts on the basilar eminences of the basioccipital and basisphenoid. These eminences are usually visible, although the exact limit of the muscle attachment is not determinable.

10. *M. digastricus*: The muscle inserts in the digastric fossa on the medial surface of the mandible (Fig. 13). The fossa is not always well defined, but in many cases the configuration of the attachment area is indicated by an elongate slightly rugose area on the surface of the bone just anterior to the postdigastric sulcus. The insertion area for *M. digastricus* could be determined for 81 of the 135 specimens examined; three of these were immature individuals, 20 were male, 21 were female and in 37 cases sex was not determined.

11. *M. mylo-hyoideus*: This muscle originates in a narrow band 2 to 3mm. wide which traverses the medial surface of the mandible from the rear of the symphysis to a point slightly below the rear of M_3 . The surface of the attachment area is often slightly roughened, but may also be indicated as a slight "break" in the medial surface of the mandible. The site of origin of *M. mylo-hyoideus* was discernible in 91 of the 135 specimens; 3 of these were immature individuals, 17 were male, 16 were female and in 55 the sex was not determined.

The results of the above considerations show that only a small percentage of the total number of muscles attaching to the cranium or mandible of the collared peccary leave sufficiently distinctive scars or rugosities that the area of attachment may be discerned with reliability. The muscles which are associated with definitive structures seem to be those involving mastication and the support of the head upon the neck. The structures to which the muscles attach are major features of the cranium,

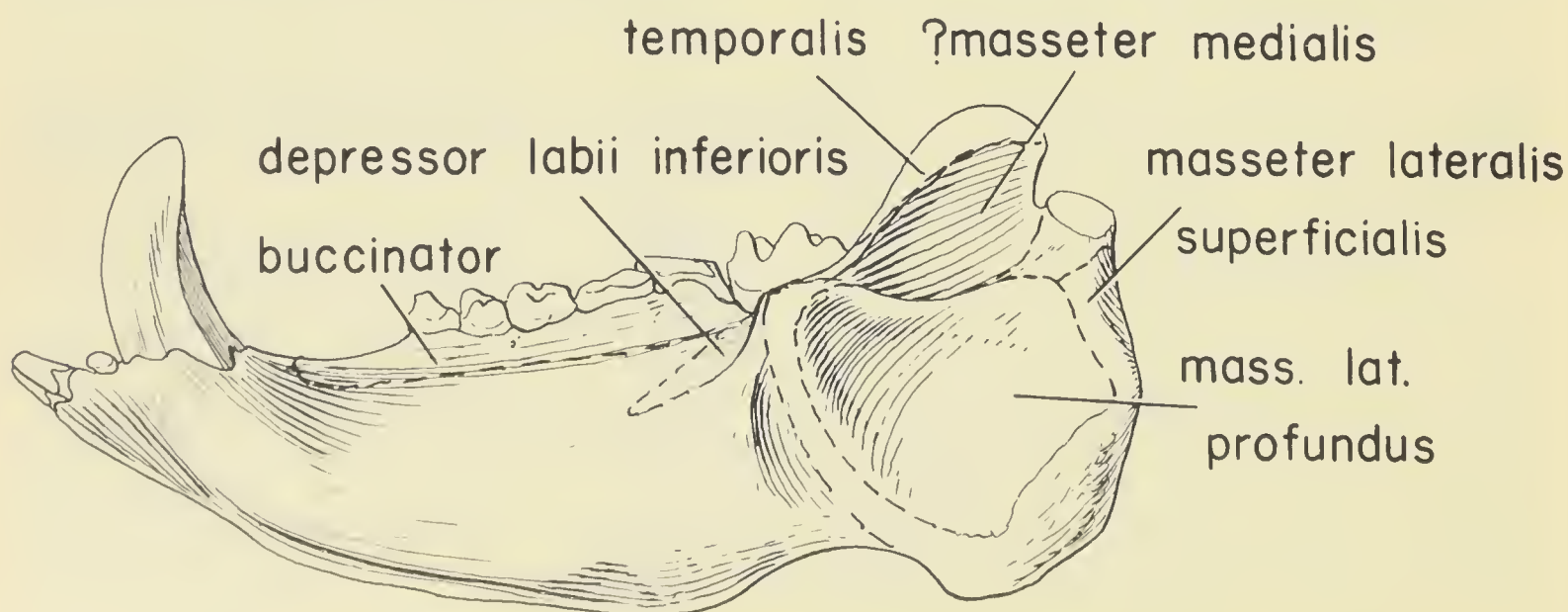


Figure 12. *Dicotyles tajacu*; lateral view of left mandible showing the attachment areas of the major muscles. About three-fourths natural size.

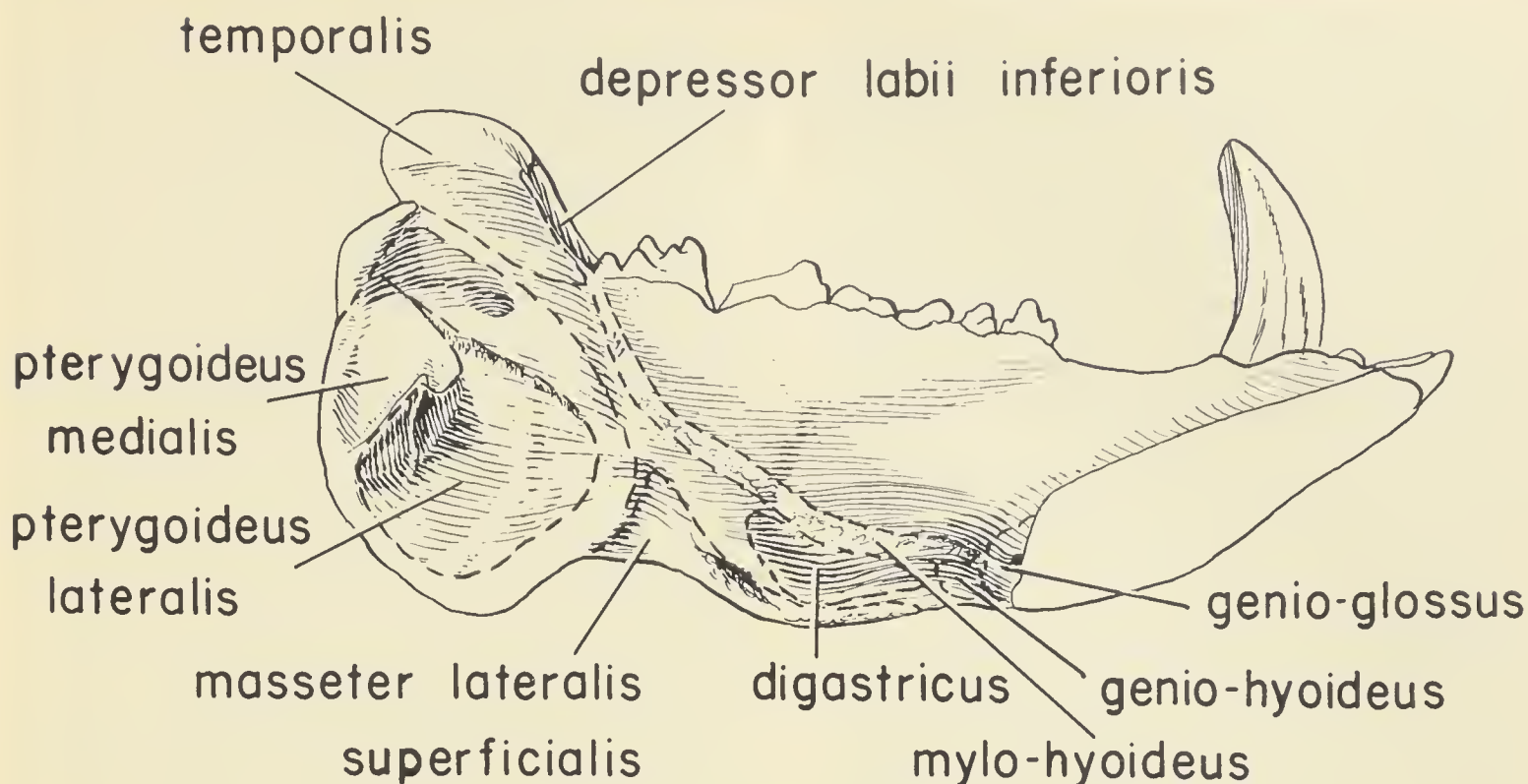


Figure 13. *Dicotyles tajacu*; medial view of left mandible showing the attachment areas of the major muscles. About three-fourths natural size.

but other, equally distinctive cranial structures seem to support more than one muscle. It is convenient, and perhaps more meaningful, to correlate a given crest or fossa with the group of muscles which are associated with it. Such a tabulation as the following may be conveniently designed:

Cranium

Occipital Aspect (Fig. 11)

Occipital fossa: Mm. rectus capitis dorsalis major and minor.

Nuchal crest: Mm. splenius capitis, rhomboideus capitis, semispinalis capitis.

Postzygomatic crest: Mm. parotido-auricularis, obliquus capitis anterior (dorsal head).

Mastoid region: Mm. longissimus capitis, splenius mastoideus, sterno-mastoideus, cleido-mastoideus, obliquus capitis anterior (ventral head).

Paroccipital process: Mm. obliquus capitis anterior, rectus capitis lateralis, digastricus (Fig. 10), occipito-hyoideus.

Lateral Surface (Figs. 9, 10)

Facial crest: Mm. depressor rostri, dilator naris lateralis.

Zygomatic arch: Mm. masseter lateralis superficialis and profundus.

Pterygopalatine fossa: M. pterygoideus lateralis.

Buccinator fossa: M. buccinator.

Temporal fossa: M. temporalis.

Ventral Aspect (Fig. 10)

Pterygoid fossa: M. pterygoideus medialis.

Condylod sulcus: Mm. rectus capitis lateralis, rectus capitis ventralis minor.

Basilar eminences: M. rectus capitis ventralis major.

Mandible

Lateral Aspect (Fig. 12)

Masseteric fossa: Mm. masseter lateralis superficialis and profundus.

Coronoid process and fossa: Mm. ?masseter medialis and temporalis.

Medial Aspect (Fig. 13)

Pterygoid fossa: Mm. pterygoideus lateralis and medialis.

Digastric fossa: M. digastricus.

Posterior surface of symphysis: Mm. genio-glossus, genio-hyoideus, mylo-hyoideus.

Mylo-hyoid line: M. mylo-hyoideus.

CRANIAL OSTEOLOGY OF THE LIVING PECCARIES

The descriptions that follow are not meant to be minutely exhaustive but rather to be a comparison of the salient features of the crania of the two species. A detailed description of the cranial elements of *Dicotyles tajacu* may be found in Rusconi (1929).

The paragraphs are numbered to facilitate comparison with similarly numbered paragraphs in the description of *Tayassu*.

Collared Peccary, *Dicotyles tajacu* (Linnaeus)
Cranium:

1. In dorsal and ventral view (Pl. 1) the greatest width of the cranium (Table 2) is usually measured across the zygomatic arches at the level of the anterior end of the glenoid fossa. The facial crest continues anteromedially from the arch and generally fades out along the rostrum posterodorsal to the canine buttress. In some specimens the facial crest is shorter and more obliquely oriented than in others, but in no case is the ventrolateral edge of the maxillary visible from dorsal view as it is in *Tayassu* (Pl. 3, Fig. 1).

2. The rostrum, that part of the cranium anterior to the zygomatic arches, is narrow and relatively deep. It tapers slightly anteriorly in dorsal view, but its outline is largely unbroken except for the prominent canine buttress. The profile of the dorsal surface of the rostrum, as seen in anterior view, is convex. Farther posteriorly, in the frontal area, the supra-orbital foramina lead anteriorly as the supraorbital-nasal canals; these converge shortly after leaving the foramina (Pls. 1, 2), but diverge again, so that the greatest width between them is measured anterior to the frontal crests, about at the level of P². Anteriorly, the canals continue onward, above the canine buttresses, to the rear of the narial notch. The latter is conspicuously more rectangular, in profile, than in *Tayassu*. The canine buttresses (Pl. 1, Fig. 2; Pl. 2, Fig. 2), developed over the roots of those teeth, are prominent, with a strongly flange-like flat anterior surface. Posterior to the buttresses the lateral wall of the rostrum is excavated to a variable degree below the facial crest, the ventral border of this concavity being formed by the linear ridge which corresponds to the upper limit of the buccinator musculature. The buccinator fossa, which extends posteriorly from the rear of the canine to a point above M¹ or, rarely, M², faces laterally.

3. In ventral view (Pl. 1, Fig. 3; Pl. 2, Fig. 3), the two pairs of incisors (the third having been lost during phylogeny) are arranged in a V-shaped array with a diastema of about 15 mm. occurring between I² and the canine. The incisive foramina are relatively large; their combined width being almost one-half of the total width of the rostrum at I². Posterior to these foramina, the surface of the palate is moderately rugose; palatine grooves seem to be developed from about P² onward, but their course is somewhat obscured and subsidiary openings in the palatal surface may occur farther posteriorly. A longitudinal median keel is often present, particularly between the canine and M³.

4. Sutures are visible only in immature individu-

als of the collared peccary, but in less fully grown individuals (deciduous premolars functional, M² erupting) it can be seen that the *premaxillaries* (Pl. 4, Figs. 1, 2; Pl. 5, Figs. 1, 2) bound the narial aperture laterally and extend posterodorsally to a point slightly (ca. 7.5 mm.) anterior to the greatest divergence of the supraorbital-nasal canals. The *nasal* bones are sharply restricted (Pl. 4, Fig. 1; Pl. 5, Fig. 1) between the premaxillaries, but still form the roof of the narial aperture. The maxillo-nasal suture is almost straight as it continues posteriorly from the premaxillary to contact the frontal. Ventrally the premaxillo-maxillary suture enters the palate through the incisor-canine diastema and extends forward to the lateral edges of the incisive foramina.

5. On the top of the cranium the *frontal* (Pl. 4, Fig. 1; Pl. 5, Fig. 1) and parietal elements have an apparently normal configuration. Depressions on the dorsal surface of the frontal above the postorbital processes are usually present, even if only to a very small degree. The fronto-nasal contact leads anterolaterally to join the maxillary; the suture of the latter with the frontal then curves posteroventrally for about 9-10 mm. to meet the jugal (Pl. 4, Fig. 2; Pl. 5, Fig. 2). The fronto-jugal suture extends posteriorly and slightly ventrally to the small lacrimal tuberosity and crosses over into the orbit, passes through the lacrimal foramen, continues ventrally and, lastly, anteriorly to enter the sphenopalatine foramen. The latter lies just dorsal and medial to the larger maxillary foramen. Just medial to the latter and ventral to the sphenopalatine foramen is a third, small, vertically elliptical aperture which probably represents the posterior palatine foramen. The frontal leaves the sphenopalatine foramen in contact, for a short distance, with the palatine, but after about 14 mm. passes posterodorsally, in contact with the larger orbitosphenoid. The frontal finally completes its circuit just dorsal to the infratemporal crests where the fronto-parietal suture meets the orbitosphenoid.

6. The posterior sutures of the *parietal* are lost in the rugosities of the nuchal and postzygomatic crests; the parietosquamosal suture extends across the temporal fossa, near its middle, to meet the alisphenoid just posteroventral to the infratemporal crest. Continuing almost vertically, the squamoso-alisphenoid suture extends downward, crosses over the ventral, pterygoid, crest of the alisphenoid to disappear near the anterodorsal base of the auditory bulla.

7. The bulla (Pl. 1, Fig. 3; Pl. 2, Fig. 3; Pl. 5, Fig. 3) is bulky, globular, but moderately acuminate anteromedially; it is composed of cancellous tissue internally and bears an anteromedially directed groove for the tympanohyal along its ventral surface. Foramina found peripheral to the bulla are: an-

teriorly, the foramen ovale; medially the median lacerate foramen; posteriorly the posterior lacerate and (just labial to it) the stylomastoid foramina. Lateral to the bulla and just behind the postglenoid process is the postglenoid foramen. A small aperture lateral to the foramen ovale probably represents the alisphenoid canal.

8. Posterior to the bulla, the squamoso-exoccipital suture descends along the posterior surface of the canal of the stylomastoid foramen, traverses the anterior base of the paroccipital process, and leads dorsally and slightly medially to join the parietal at the postzygomatic crest.

9. Anteriorly, the squamosal contacts the *jugal* at the anterior edge of the glenoid fossa. The bone is excavated laterally and flares outward below and anterior to the orbit. The postorbital process of the jugal may approach, but does not meet that of the frontal. There is nothing unusual regarding the relations of the jugal to the surrounding bones. The ventral surface of the jugal, and part of the adjacent maxillary, supports the origin of the masseteric musculature. The area of attachment is an elongate surface, beginning at the anterior end of the glenoid fossa, which broadens in its anterior third before terminating behind the site of origin of the depressor snout muscles (Pl. 1, Fig. 3; Pl. 2, Fig. 3). The point at which these two muscle masses meet (along and medial to the facial crest above M^1 or M^2) is often marked by a pointed or spinous process. The sites of origin for both of these muscle groups face generally ventrally and are largely hidden in lateral view by the strong, thick zygomatic crest which projects somewhat ventrally. The site of origin for *M. masseter lateralis profundus* in particular is somewhat higher, relative to the level of the alveolar border (and to that of the origin of *M. buccinator*) than in *Tayassu*.

10. In lateral view the facial crest follows the ventral edge of the jugal below the orbit and curves smoothly upward above infraorbital foramen toward the point of maximum divergence of the supra-orbital-nasal canals. In most specimens of *Dicotyles* the anterior curvature of the facial crest is slight. As mentioned above, the crest is nearly straight, but oblique, in dorsal view. Medial to the crest, the site of the origin of the depressor snout muscles is an anteriorly tapering ventrally facing concavity.

11. Within the orbit, the *lacrimal* is slender dorsally, but broadens ventrally and does not enter the maxillary foramen. In facial aspect the lacrimal is slightly exposed below the lacrimal tubercle.

12. The *maxillary* lies on the lateral surface of the snout and face. Its contacts with other bones of the cranium are rather ordinary and will not be described further. On the lateral surface of the bone, the

infraorbital foramen lies over P^4 or, in some instances, M^1 (Pl. 1, Fig. 2; Pl. 2, Fig. 2). In cross section the foramen is wide, and nearly circular. Below the foramen, the ridge indicating the dorsal extent of *M. buccinator* diminishes in magnitude as it continues posteriorly. In ventral view, the edges of the palate are constricted conspicuously relative to the strong canine buttresses (Pl. 1, Fig. 3; Pl. 2, Fig. 3). The cheek teeth are slightly bowed outward, the greatest point of separation being between the inner edges of M^1 . In overall trend, the cheek teeth also diverge progressively from front to back, the distance between the anterolingual alveoli of M^3 usually being greater than that for the lingual alveoli of P^2 .

13. Even in young specimens, the maxillo-palatine suture is not visible. Otherwise, the slightly concave palatal surface is distinguished by the longitudinal median keel, mentioned above, and by a number of small nutrient foramina which dot the bone just medial to cheek tooth alveoli. Posterior to M^3 , a small, semicircular posterior palatine notch is incised between the maxillary tuberosity and the pterygoid ramus of the palatine bone. Between the last molars the surface of the palatine is nearly flat, being marked in some specimens only by a narrow median longitudinal groove which deepens posteriorly toward the choanal fossa. Posteriorly, the *palatine* overlaps the pterygoid which is inserted between the latter and the alisphenoid. In lateral view, the palatine, in contact with the alisphenoid, extends dorsally into the pterygopalatine fossa and then anteriorly, first in contact with the orbitosphenoid, and second, with the frontal, into the sphenopalatine foramen.

14. The *pterygoid* is a thin, ventrally tapering element which is inserted between the palatine and alisphenoid bones near the anterior end of the rather narrowly V-shaped choanal fossa. The pterygoid does not extend laterally into the pterygopalatine fossa.

15. The posterior contact of the *alisphenoid* with the frontal has already been discussed. Just below the infratemporal crest, the alispheno-frontal suture enters the large anterior lacerate-rotundum foramen which is situated just medial to the infratemporal crests. The smaller optic foramen is situated antero-dorsal to the anterior lacerate-rotundum foramen. The alispheno-orbitosphenoid suture leads anteriorly out of this foramen to contact the palatine about 30 mm. farther on and lies ventral and medial to a rather sharply developed linear eminence which leads posteriorly from the roof of the sphenopalatine foramen and fades out toward the optic foramen. The development of this eminence, the bony covering of the ethmoidal sinus, is variable; the lateral surface is generally broadly ridgelike, but occasion-

ally it may be flat with a prominent but moderately broad, ventrally projecting crest. In either case, this eminence forms the dorsal border, and the flared ventrolateral edge of the alisphenoid forms the ventral border, of the elongate pterygopalatine fossa. This fossa contains the origin of *M. pterygoideus lateralis*. *M. pterygoideus medialis* originates along the flat ventral surface of the alisphenoid, anterior to the bulla.

16. Between the bullae, the basioccipito-basisphenoid contact is not visible, but the basilar eminences are probably developed across this suture. The eminences (Pl. 1, Fig. 3; Pl. 2, Fig. 3) are a pair of prominent spindle shaped, longitudinally elongate structures which support the insertion of *M. rectus capitis ventralis major*.

17. Posterolateral to the eminences and anterior to the condyles are the condyloid foramina. Lateral to these, the paroccipital processes, formed largely of the *exoccipitals*, project posteroventrally, tapering toward their tips. The latter are about on a level with the tips of the postglenoid processes, which lie slightly above that of the cheek teeth.

18. Dorsally, on the occipital surface, the contact between the *exoccipitals* and the *supraoccipital* is not determinable. Medial to the external auditory meatus and just below the tip of the postzygomatic crest, a small process is variably developed. It is associated with the insertion of *M. rectus capitis dorsalis minor*. The external auditory canal and meatus is apparently backed by the squamosal. The *mastoid* is not visible externally. Dorsally and medially the flange-like edges of the lambdoidal and postzygomatic crests bound the occipital fossa which chiefly houses the insertion of *M. rectus capitis dorsalis major*.

Mandible:

19. In general the profile of the mandible is long and low (Pl. 5, Figs. 4, 5). The symphysis curves upward from below P_2 , then is procumbent anterior to the canine. The incisors extend forward from the anterior tip of the symphysis, the first and second pairs forming a slightly concave occlusal shelf anterior to the third. There is no diastema between I_3 and the canine. The latter projects almost vertically from its alveolus and is slightly splayed laterally (Pl. 6, Fig. 3). The diastemal crests behind the canines are narrow, but not sharp, and rise slightly toward the anterior edge of P_2 . Mental foramina lie below the diastemal crest, one or two below P_2 and another about midway between P_2 and the canine. Posterior to this the horizontal rami are narrow with steep lingual and labial surfaces. A slight convexity on the labial surface of the body of the ramus begins below M_1 and rises posteriorly toward the temporal fossa of the coronoid process. Below the premolars, the

ventral edge of the ramus is essentially straight, but the postdigastric sulcus forms a broad, shallow concavity between the anterior portion of the mandible and the angle. The peripheral border of the angle is broadly rounded; the condyle sits slightly anterior to the posterior border of the angle.

20. Anterior to the condyle, the temporal fossa occupies the labial surface of the coronoid process and is separated by a rather low ridge from the insertion area of *M. masseter lateralis* (Pl. 5, Figs. 4, 5). As mentioned previously, this so-called temporal fossa may house, at least in part, fibers of *M. masseter medialis*. In dorsal view (Pl. 6, Fig. 3) the condyle is somewhat tear-shaped with a pointed lingual tip and a broader labial extremity. The anterior edge of the ascending ramus forms a progressively widening shallow sulcus toward the rear of M_3 ; the sulcus houses the origin of *M. depressor labii inferioris* and (in part) *M. buccinator*, the fibers of the two muscles being inseparable at this point. The cheek teeth are aligned in a linear fashion, each tooth row diverging slightly from the other from front to back. The dorsal surface of the symphysis rises from the genial pits at an angle of about 30° ; in cross section the dorsal surface of the symphysis is narrowly concave.

21. The paired genial pits are low, on the posterior surface of the symphysis, and lie just above a poorly developed, median, genial spine. On the lingual surface of the mandible, a narrow, flat, smooth to variably roughened line can often be followed posterodorsally from the genial pits, above the digastric fossa to just below the rear of M_3 . This is the line of attachment of *M. mylohyoideus*. Just below this, and below M_1 - M_3 the lingual surface of the mandible is excavated by the concave, anteriorly tapering, digastric fossa. Posterior to the latter, the usually flat, but variably roughened lingual surface of the angle contains the insertion of the pterygoideus muscles. Above this, the mandibular foramen separates the insertion areas of the pterygoideus muscles (below) and the temporalis muscles (above).

22. In ventral view (Pl. 6, Fig. 1) the horizontal rami diverge from the symphysis at an angle of about 15° . The anteroventral tip of each angle is inflected medially out of line with the overall trend of the ramus, although the degree of inflection is variable. The ventral border of the postdigastric sulcus is narrow, but not sharp. Anteriorly, below the premolars, the essentially flat ventral surface slants slightly dorsolaterally.

White Lipped Peccary, *Tayassu pecari* Fischer

The numbering of the paragraphs in this section corresponds with that in the preceding section. Features not explicitly mentioned below can be

considered to generally resemble their counterparts in *Dicotyles*. In the following description, points of difference between the two forms are emphasized.

Cranium:

1. As in *Dicotyles* the greatest width of the cranium is measured (Table 8) at the anterior edge of the glenoid fossa, but the zygomatic arches, although essentially straight, taper anteriorly more conspicuously (Pl. 3, Figs. 1, 3) than in the collared peccary. In dorsal view (Pl. 3, Fig. 1), the ventrolateral edge of the maxillary projects laterally beyond the facial crest in *Tayassu*.

2. Instead of being excavated, the rostrum expands laterally, partially concealing the mass of the canine buttress which is, in addition, less robust than in *Dicotyles*. Along the undersurface of this linear swelling, which probably conforms to an expanded maxillary sinus, the attachment area of M. buccinator is developed as an elongate, ventrally facing concavity which tapers posteriorly to P⁴ or M¹ (Pl. 3, Figs. 2, 3). The dorsal surface of the rostrum is generally flatter in *Tayassu* than in *Dicotyles*. The supraorbital foramina are situated similarly in the two genera, but in *Tayassu*, the canals almost always diverge immediately upon leaving the foramina; occasional convergence (Pl. 3, Fig. 1) is of lesser magnitude and occurs nearer the foramina than in *Dicotyles*. The anterior extremities of the supraorbital-nasal canals are not as well defined as in the collared peccary, and the posterior profile of the narial notch (Pl. 3, Fig. 2) is conspicuously more acuminate in *Tayassu*. The canine buttress is not only less robust than in *Dicotyles*, but its vertical dimension is less.

3. In ventral view (Pl. 3, Fig. 3), the incisor pairs are arrayed in a V-shaped configuration as in *Dicotyles*, but the diastema between the incisors and canines is about 20 mm. The incisive foramina are relatively smaller than in *Dicotyles*, their combined width being only about one-third the width of the rostrum at I². Posteriorly, the surface of the palate is smooth and flat although it may bear a series of obliquely transverse grooves and ridges which reflect corrugations in the soft palate. The narrow palatine grooves emerge opposite the rear of the canines. A median longitudinal keel is not present.

4. Sutures are often visible in individuals with a complete but little worn dentition. The premaxillaries (Pl. 4, Figs. 3, 4) tend to be slender and more evenly acuminate posteriorly in *Tayassu*; the width of the nasals is not restricted between the premaxillaries as seen in *Dicotyles*. The combined line of contact between the nasals and the premaxillaries is straight. It diverges posteriorly only before contacting the frontal. The premaxillo-maxillary contact on the palatal surface is as in *Dicotyles*.

5. In dorsal view (Pl. 4, Fig. 3) the contact between the frontal and parietal elements in *Tayassu* is much like the condition in *Dicotyles* except that in the former genus the fronto-parietal suture reverses direction and projects farther anteriorly at the midline. The fronto-nasal contact resembles that of *Dicotyles*, but the short maxillo-frontal suture seems to be directed more vertically in *Tayassu*. Whereas the maxillo-jugal suture in *Dicotyles* curves gently posterodorsally behind the facial crest to contact the frontal, the same suture in *Tayassu* is sharply angulate (Pl. 4, Fig. 4).

6, 7 and 8. The description of *Dicotyles* given in these paragraphs would not have to be significantly altered to apply to *Tayassu*.

9. In contrast to *Dicotyles*, the jugal is not excavated laterally and does not flare outward below the orbit in *Tayassu*. The differences in the maxillo-jugal suture in the two genera have been noted above. The site of origin of M. masseter lateralis superficialis and profundus faces ventrolaterally in *Tayassu*; the zygomatic crest is not broad and does not project ventrally as strongly as in *Dicotyles*. The origin of the depressor snout muscles occurs markedly dorsal to that for the masseteric muscles in *Tayassu* and lies at a level conspicuously higher than of the alveolar border.

10. The facial crest is not smoothly continuous with the crest of the zygomatic arch, but diverges sharply upward (Pl. 3, Fig. 2; Pl. 4, Fig. 4). The profile of the cranium in dorsal view is usually more sharply constricted anterior to the zygomatic arch in *Tayassu* than in *Dicotyles*. The area of origin of the depressor snout muscles in the former genus is oriented anterodorsally; it is broadly triangular and faces nearly directly anteriorly in sharp contrast to the condition in *Dicotyles*.

11. *Tayassu* and *Dicotyles* are generally similar in the features described in this paragraph.

12. On the lateral surface of the maxillary, the infraorbital foramen lies above P⁴ or M¹. The cross section of the foramen is narrow and slit-like. The configuration of the attachment area for M. buccinator has been described in paragraph 2. *Tayassu* also differs from *Dicotyles* in that the palate is not sharply constricted in the diastemal region. Furthermore, while the cheek teeth diverge slightly posteriorly, the tooth rows are not as bowed outward as in *Dicotyles*, and are set closer together relative to the width of the cranium.

13 and 14. The palatine and pterygoid bones of *Tayassu* are much like those in *Dicotyles* except that a broad, moderately deep ovoid depression occurs on the palatal surface between the last molars and extends posteriorly toward the anteroventral edge of the choanal fossa.

15. Many of the features of this paragraph are similar in the two genera. The *orbitosphenoid*, however, has an elongate slender neck in *Tayassu* which extends into the anterior portion of the pterygopalatine fossa below the crest which forms the dorsal border of the latter. In *Dicotyles* this crest is slightly more ventral in position and the posterior portion of the orbitosphenoid is larger and broader. In *Tayassu* the attachment area for *M. pterygoideus medialis* is broader and flatter than in *Dicotyles*.

16. Between the bullae, the basioccipito-basisphenoid contact is a nearly straight transverse line. The basilar eminences (Pl. 3, Fig. 3) are not as strongly developed, not as linear and not as readily differentiated from each other as in *Dicotyles*.

17. The condyloid foramina are similar to those of *Dicotyles*.

18. The exoccipito-supraoccipital suture emerges from the anterolateral corner of the foramen magnum and continues dorsolaterally to reach the squamosal just ventral to the squamoso-parietal suture. The small process which may be developed in association with *M. rectus capitis dorsalis minor* in *Dicotyles* has not been observed to occur in *Tayassu*. The occipital fossa, bounded by the lambdoidal and postzygomatic crests is not as broad as in *Dicotyles*.

Mandible:

19. The profile of the mandible in *Tayassu* (Pl. 5, Fig. 6) is generally longer and shallower below P_2 than in *Dicotyles*. The profile of the symphysis is not as strongly curved upward, the dorsal and ventral borders are usually more nearly parallel, the concavity below the canine is not as pronounced and the first two pairs of incisors emerge from the symphysis at a somewhat steeper angle than in *Dicotyles*. The diastemal crests tend to be sharper in *Tayassu*, and below these, the mental foramina are slightly posterior to their position in *Dicotyles*. In *Tayassu* the horizontal rami are more massive and swollen, particularly just below the alveolar border on either side of the mandible. The ventral profile of the mandible in *Tayassu* is not as straight below the premolars to the rear of M_2 as in *Dicotyles*.

20. The features described in this paragraph are comparable in *Tayassu* and *Dicotyles* except that in the former the cheek tooth rows are set relatively closer together.

21. The major difference here between *Tayassu* and *Dicotyles* is that the ventral border of the mandible tends to be deflected inward below the digastric fossa in the white lipped peccary.

22. The degree of divergence of the rami in *Tayassu* is about the same as that in *Dicotyles*, but the

angle of the mandible is not inflected (Pl. 6, Fig. 2) in the former genus. The ventral border of the postdigastric sulcus thickens anteriorly in *Tayassu* in contrast to the uniformly narrow edge of this sulcus in *Dicotyles*.

Variation:

Inspection of the more than fifty crania of *Tayassu pecari* in the Department of Mammalogy of the American Museum of Natural History indicates that this genus is subject to a kind and degree of osteological variation similar to that which was noted for *Dicotyles tajacu*. Each species shows little variation, other than general robustness, which can definitely be correlated with sex (compare male and female canine dimensions, Table 10). With respect to ontogeny, it is interesting to note that features of the dentition and various sutural relationships are the most useful means for separating immature crania (with only the deciduous dentition in place) of the two species. Only in crania of older individuals do the characteristic crests and ridges of the rostral and adjacent areas become expressed to a degree approaching the adult condition, and from the time that the first or second permanent premolars are fully erupted, such characters are essentially completely developed.

Comparison of Tables 2 and 6 with Tables 8 and 12 shows that in 12 out of 16 dimensions, the range observed for the *Tayassu* sample overlaps that observed for *Dicotyles*. In three of the 12 instances (i.e., width between M^3 alveoli, depth below P_2 and the width between the alveoli of M_3) the degree of overlap is quite large. In two out of the twelve cases the degree of overlap is quite small (I^1 to condyle length and I_1 to condyle length). In the remaining four cases (least rostral width, height from condyles to nuchal crest, breadth between the postorbital processes, and depth from the coronoid process to the angle of the mandible) the observed ranges for each sample do not overlap. In most cranial and mandibular dimensions the mean calculated for the *Dicotyles* sample is 10 to 20 per cent smaller than that calculated for *Tayassu*. Important exceptions to this are: the length of the upper post-canine diastema (*Dicotyles* is 30 per cent smaller), the least width of the rostrum (*Dicotyles* is 47 per cent smaller), and the length of the lower post-canine diastema (*Dicotyles* is 27 per cent smaller). The mean depth of the mandible below P_2 is 95 per cent of that below M_3 in *Dicotyles* as compared with 89 per cent in *Tayassu*. While this difference is small it confirms the impression gained when the measurements were being made that the mandibular ramus is proportionally shallower anteriorly in *Tayassu*.

DENTAL CHARACTERISTICS OF THE LIVING PECCARIES

Dicotyles tajacu Upper Dentition

Deciduous teeth (Pl. 5, Fig. 3). As in the case of the permanent premolar dentition, molar cusp terminology is used for convenience, but not necessarily to indicate homology. The deciduous first incisors are spatulate, small versions of the permanent tooth, but compared with its successor, dl^2 is simpler, and lacks the basal inner cingulum. Variation encountered with respect to these teeth chiefly involves degree of robustness. Also, in some specimens a slight increase in the size of dl^2 relative to that of dl^1 has been observed.

The deciduous canine is an elongate, slightly compressed and barely recurved tooth which protrudes from its alveolus at a much shallower angle than does the nearly vertical permanent tooth. The deciduous tooth is unmarked by ridges or crests and tapers gradually apically.

The deciduous second premolar is triangular in outline, the apex of which is anterior. A pair of labial cusps are the major features of the crown, the second, or metacone, being set somewhat posterolabial to the paracone. A subsidiary, conical protocone is incipiently developed immediately posterolingual to the latter. Posterior to this is a lower, but more distinct, conule. A posterior cingulum traverses the heel and curves around the lingual side to reach the base of the protocone. Anterior to the latter, a cingulum extends to the narrow tip of the tooth. Intraspecific variation has been observed in the following features: the degree of triangularity of the basal outline; the presence or absence of an oblique crest extending anterolingually from the base of the metacone; the degree of prominence of the heel area lingual to the metacone; the position of the protocone relative to the paracone; the size of this and the following tooth relative to that of dp^4 .

The deciduous third premolar is more molariform than the preceding and has a well developed paracone, metacone and hypocone. The protocone is still in a relatively incipient stage and lies along the lingual base of the paracone. The V-shaped transverse valley is unobstructed; the rather pyramidal cusps are not connected into lophs. The anterior and posterior cingula are relatively short; small labial and lingual cingula occur at the transverse valley. The posterior moiety is wider than the anterior moiety. In some specimens, the protocone is situated more posterolingually, a small conule occurs between the protocone and metacone, and the posterior

cingulum is continuous around to the anterior edge of the transverse valley on either side of the tooth.

In contrast to the preceding tooth, dp^4 is completely molariform and is a slightly smaller replica of M^1 . In general, the cusps of the deciduous dentition were observed to be conical and rather bunodont, although in a number of instances teeth were noted to have cusps which were steeper and more pointed.

Permanent teeth: The first incisor (Pls. 1, 2; Table 3) is a robust spatulate tooth with a smooth convex outer surface and concave inner surface, bordered by a basal cingulum. In unworn teeth, one or more weak crests extend from the cingulum to the apex along the mid-posterior surface. The second incisor is smaller than I^1 , although the sizes of the two teeth are variable with respect to one another. Also, I^2 has a convex outer surface and an inner basal cingulum, but, in contrast to I^1 , the high shearing crest is located above the longitudinal midline of the tooth rather than being recurved lingually. In unworn teeth the apex of the crest may be posteriorly recurved. The shearing crest of I^2 was seen to be incipiently divided into a larger anterior, and a smaller posterior, conule in only a few specimens.

The canine (Pls. 1, 2) is slightly recurved, and extends nearly vertically from its alveolus. In cross section, the outline of the tooth is triangular with the apex posterior. The flat anterior surface is emphasized as wear progresses. A slightly recurved groove, flanked by low ridges, extends apically along the mid-labial surface; a similar configuration is usually found on the labial surface as well, although the degree to which these grooves and ridges are developed on either surface is variable. As shown in Table 4, the mean length and width of the canines of male individuals is slightly greater than for females. This sexual dimorphism, while not marked, apparently causes the rather high values for the coefficient of variation (V) when calculated for the whole sample.

The second premolar (Pls. 1, 2, Pl. 7, figs. 5-7) is subtriangular in outline with a narrow, but rounded anterior tip and a broad heel. A prominent paracone is separated by a narrow transverse valley from the smaller metacone. The labial cingulum is absent, but the anterior cingulum extends around to the lingual side. The posterior cingulum extends around to the posterolabial base of the metacone. A protocone of variable size lies posterolingual to the paracone and in some instances a subsidiary swelling of the cingulum occurs anterior to the protocone. A small conule may be developed between the metacone and the protocone, or the metacone may be reduced and incorporated into the anterior member of a pair of anteriorly concentric crests which traverse the heel

(Pl. 2, Fig. 3). Other variations observed in P² include its size relative to P³ and the degree to which the paracone and protocone are emphasized to the detriment of the elements of the heel. As shown in Table 5, the range of the dimensions of P² overlaps that for P³. However, observations made on 80 specimens revealed that within each individual, P² is definitely smaller than P³. Whether the width measurement is taken through the paracone or the metacone is dependent upon the position of the protocone relative to those cusps and the degree of development of the anterolingual cingulum. In 41 out of 52 cases, the greatest width of P² was measured through the metacone; in 11 cases the measurement was made through the paracone.

The third premolar is more molariform, with the protocone being only slightly less well developed than the paracone and larger than the metacone. Occasionally, however, the bulk of the metacone equals that of the paracone (Pl. 7, Fig. 6). A small cusp usually occurs lingual to the metacone; this should be designated as the metaconule because in some cases, a distinct hypocone is developed from the lingual cingulum. A small protoconule is usually present. An anterior cingulum is continuous from the base of the protocone to the labial side of the paracone and a posterior cingulum is similarly developed around to the labial base of the metacone. As in P², the heel can be differentiated into a pair of parallel anteriorly concave lobes, the posterior of which curves around to the rear of the protocone, and in this case the metacone is reduced to little more than a slight swelling. The dimensions of all P³'s measured are summarized in Table 5. In one out of 80 cases was P³ found to be longer than the adjacent P⁴. In none of these individual specimens was P³ observed to be wider than P⁴. The point of measurement of the greatest width of P³ is governed by the same variables as in P². In 39 of 54 specimens the greatest width was measured through the paracone; in 12 specimens through the metacone and in 3 specimens the measurement was the same for either alternative.

The last premolar is essentially similar to, but larger than P³. The configuration of the cusps is the same, but the cusps are larger. As in P³, P⁴ is broader across the anterior moiety than across the posterior moiety although the degree of reduction of the latter is variable. Other variations are similar to those encountered in P³. Dimensions for P⁴ are also given in Table 5. As for P³, P⁴ was found to be longer than the succeeding tooth of the series (M¹) in only one out of the 80 specimens. On the other hand, in 24 of the 80 specimens, P⁴ was wider than the adjacent M¹. The site at which the maximum width of P⁴ is measured varies chiefly with the prominence of the

cusps and cingulum in the posterolingual quadrant of the tooth. Thus, in 45 out of 54 instances, the maximum width of the tooth was measured through the paracone, in 6 through the metacone and in 2 cases the widths for the two alternatives were equal.

The first molar is subquadrangular in outline. All four major cusps are well developed, the paracone and metacone being slightly anterior to their lingual counterparts. A sinuous transverse valley separates the anterior moiety from the posterior moiety, and is somewhat interrupted, in labial profile, by the metaconule. Short basal crests from the antero- and posterolingual corners of the protocone meet similarly short crests from the paracone. Those contributed by the anterior base of each cusp unite in the low protoconule which is basally fused to the anterior cingulum. The latter extends from the protocone around to the anterolabial base of the paracone. Basal crests similar to those of the protocone are developed from the hypocone, the anterior of these being the metaconule. The metacone is simply conical. A posterior cingulum extends from the hypocone to the posterolabial base of the metacone. Labial and lingual cingula are present or absent.

The second molar is larger than the first, has a strong labial and an incipient lingual cingulum, but is otherwise as M¹. In M³, the cingula are better developed and the tooth tapers more conspicuously posteriorly than in M¹ or M². The second molar is usually the largest of the cheek teeth.

The ranges for the dimensions of the upper molars are given in Table 5; some overlap between analogous dimensions of successive teeth can be observed. On an individual basis, however, M¹ was never observed (in 80 specimens) to be longer than M² while M² was longer than M³ in only 11 cases. The length of M² equalled that for M³ in only two of the 80 specimens. Regarding the molar widths, M¹ was wider than M² in only one out of 80 individuals, but M² was wider than M³ in 72 cases. The width of the molars is usually greatest across the anterior moiety. The reverse was true in only one of 53 cases for M¹ and was never observed for M² or M³. The width of the posterior moiety equalled that of the anterior moiety only once in 50 cases for each of the upper molars.

As far as other features are concerned, the upper molars of *Dicotyles tajacu* often show increased hypsodonty and sharpness of the cusps, and emphasis and anterolabial elongation of the protoconule and metaconule. In a number of instances, labial cingula become more strongly developed and occasional increase in the breadth of the posterior cingulum has been noted. In a few specimens, M² tapers conspicuously posteriorly (Pl. 7, Fig. 5) and extreme

examples of this have been observed in M^3 . An extra, anteriorly concave crest has been found on M^3 between the base of the metacone and the posterior cingulum. Because the lengths of the upper cheek teeth are subject to ontogenetic intertooth wear, the widths of the teeth would seem, from theoretical considerations, to be the most stable dimensions available for comparison with other samples. However, inspection of Table 5 reveals that except for M^3 the coefficient of variation (V) for the width of any given member of the cheek tooth series is greater than that for the length. In general, the dimensional variability of the premolars is greater than for the molars. As would be expected, the length of M^3 has the greatest variability of the molar dimensions.

Lower Dentition

Deciduous teeth: The deciduous incisors are essentially small models of the mature teeth, with dI_2 being the largest. The third incisor is considerably simpler than its permanent replacement.

As in the upper dentition, the deciduous canine is a simple, apically tapering slightly recurved tooth which emerges from its alveolus at a shallower angle than does the permanent tooth. It is also splayed outward more than the latter.

In dP_2 a large main cuspid is located slightly anterior to the central position on the crown and is bounded anteriorly by a small conulid and posteriorly by a simple talonid. Both the size of the anterior conulid and the complexity of the talonid are variable. A crest begins at the apex of the main cuspid, passes down along the posterolingual edge and curves labially across the base to join the talonid at the posterolabial corner of the tooth. In a few cases, incipient bifurcation of the main cuspid has been observed.

In dP_3 , which is larger and more elongate than dP_2 , the central cuspid is transversely bifid with a lingual connection to the talonid. The latter is composed of two or more cuspids, aligned transversely. The anterior basal conulid of the tooth is better developed than in dP_2 and is associated with one or more accessory conulids. In some individuals, the accessory conulids are stronger and the tooth tapers abruptly rather than gradually anterior to the central pair of cuspids.

The three transverse pairs of cuspids of dP_4 seem to be typical of peccaries, as well as of other artiodactyls. The anterolingual cuspid is conical, but its labial counterpart bears a short basal posterolingual crest which terminates at the transverse valley between the first and second pair of cuspids. In some specimens, a crest leads anterolingually from the

cuspid under discussion and terminates at a low, median anterior conulid. In the second, or central row of cuspids, the labial protoconid bears two short basal crests, one of which leads anterolingually, the other posterolingually. Each meets a corresponding crest from the metaconid. In the final row, the lingual cuspid, or entoconid, is conical, but the hypoconid bears antero- and posterolingually directed crests, the latter being formed into the hypoconulid. A posterior cingulum extends between the hypoconid and entoconid. In dP_4 , individual variation involves sharpening of the cuspids, accentuation of the accessory conulids and the abrupt, rather than gradual, anterior tapering of the tooth.

Permanent teeth: The first two incisors (Pls. 5, 6) are procumbent, elongate teeth which combine to form a slightly concave spatulate surface. Posterior to this, I_3 is a short low tooth with a slightly oblique sectorial crest. Differences in actual size are the main form of variation in the incisor dentition. The third incisor is often reduced and simple. Dimensions of I_{1-3} are presented in Table 3.

The canine has a triangular occlusal outline with a concave posterior surface. The lingual surface is smooth but a weak, recurved groove, bounded anteriorly by a low ridge, ascends the labial surface. Variation involves the actual size of the tooth and the degree to which the lateral grooves and ridges are developed. Compared with that of *Tayassu*, the canine of *Dicotyles* is relatively more hypsodont and considerably slenderer.

The first premolar of the permanent series, P_2 (Pls. 5, 6, 7, Figs. 1-4), is constructed essentially as its deciduous predecessor with the exception that labial and lingual crests on the posterior surface of the main cuspid are usually better developed. The main cuspid may or may not be twinned, and in the single condition, its cross sectional mass may be relatively great. In some individuals which are usually, but not always, members of the subspecies known as *Dicotyles tajacu angulatus* (Pl. 7, Fig. 1), the premolar teeth are large and quite hypsodont with the cuspids of the talonid being greatly reduced relative to those of the trigonid. Considering *D. tajacu* as a whole, the talonid is composed of two or three conulids arranged in a transverse row; a median conulid usually lies in front of these and may develop into a transversely extended arm. Absence of this conulid results in a basin bounded anteriorly by the trigonid and posteriorly by the cuspids of the talonid. The basin may be open lingually, but it is usually closed off labially. In 81 instances, P_2 was neither longer nor wider than P_3 in the same individual although in the total range of the sample (Table 7) the dimensions for the two teeth do overlap. The width of the trigonid varies relative

to that of the talonid to the extent that in 11 of 54 cases the maximum width of P_2 was measured across the trigonid. In three of these cases the two alternative widths were equal.

Except for being relatively broader, and having a more distinct separation of the labial and lingual components of the main cuspid and of the anterior basal conulids, P_3 is much like dP_3 . Variations in P_3 , which are similar to those observed in the preceding tooth, include relative expansion of the heel, proliferation of its cuspids (Pl. 7, Fig. 3) as well as a considerable increase in the height of the main cuspid. In 81 observations, P_3 was never seen to be longer than P_4 . The frequency with which the trigonid is wider than the talonid in P_3 is about the same as for P_2 . Thus, in 55 observations, only 10 instances were noted in which the trigonid was wider and in two instances the trigonid and talonid were of equal width.

The permanent P_4 is, of course, strikingly different from dP_4 . The former is a submolariform tooth with components which may be identified as protoconid, metaconid, hypoconid and entoconid. The cuspids of the anterior moiety are higher and more strongly developed than those of the posterior moiety. A small conulid usually lies athwart the bases of the protoconid and metaconid anteriorly, while posteriorly, each of these cuspids gives rise to a short basal longitudinal crest. These crests, in conjunction with a smaller pair contributed by the hypoconid and entoconid, obstruct the transverse valley. Between the hypoconid and entoconid a small hypoconulid (Pl. 7, Figs. 2, 4) usually occupies the posterior midline of the tooth, but may come to lie behind the hypoconid. The crest which extends along the posterior surface of the protoconid may become enlarged to the detriment of its lingual counterpart; this is associated with an alteration of the cuspids of the talonid into a cross-shaped configuration. Another variation on this theme is the emphasis and transverse elongation of the posterior crest from the protoconid, the loss of its lingual partner, the reduction of the anterior crest from the entoconid and emphasis and anterolingual elongation of that from the hypoconid (Pl. 7, Fig. 4). A conulid may develop from the labial cingulum at the transverse valley; a crest-like continuation of the posterior cingulum usually leads from this conulid to the hypoconulid. The configuration just described is associated with an increase in the width of the talonid (Pl. 7, Figs. 2, 3). In contrast to the upper dentition, P_4 is only rarely longer or wider than the adjacent M_1 , the incidence for this being, respectively, four and three cases out of 81. In one additional instance, P_4 was as long as M_1 . The degree of molarization of P_4 closely approaches that of M_1 and in 51

out of 53 instances the width of the trigonid was observed to be greater than that of the talonid. In none of these instances were two alternative widths equal. The ranges of the dimensions of P_4 in terms of the total sample are summarized in Table 7.

In M_1 the four major cuspids are well developed. Between those of the anterior moiety and the posterior moiety is the sinuous transverse valley. The tooth has a strongly bilobate occlusal outline because neither a labial nor a lingual cingulum is present at the ends of the valley. Anterior and posterior cingula are short. The protoconid gives rise to a short, anterolingually directed, basal crest which ends at the anterior cingulum; the metaconid gives rise to a short posterolabially directed basal crest which terminates at the transverse valley. Directly posterior to this is a short crest from the base of the hypoconid. The entoconid is subconical with a slight labial basal expansion toward the hypoconid. A small, conical hypoconulid merges with the posterior cingulum, and is connected, to a variable degree, to the hypoconid.

The second and third molars are constructed as in M_1 except that in M_3 the hypoconulid is expanded posteriorly with a large terminal cuspid and a variable number of smaller conulids anterior to it. The heel of M_3 is usually narrow, but it may be squared off and broad (pl. 7, Fig. 4). Usually, there is a single median conulid posterior to the hypoconid and entoconid; behind this are a pair of larger conulids each of which may be joined by crests to the anterior conulid (pl. 7, Fig. 2). In other cases two median conulids are aligned behind the "hypolophid" and in some instances, three conulids are transversely arrayed across the tip of the heel, being separated from the "hypolophid" by a single small conulid. The last molar is usually narrower than M_2 , but this is variable. Other variations in the configuration of the lower molars include minor additional complexities, the addition of labial cingula, the presence of a distinct conulid at the anterolingual base of the metaconid, and an increased hypsodonty of the cuspids. The ranges of the dimensions of the lower molars are presented in Table 7. Within individual specimens (81 cases) M_1 was never longer nor wider than M_2 , and M_2 was never longer than M_3 . However, M_2 was wider than M_3 in 68 cases. The talonid of M_1 is usually (50 of 58 cases) wider than the trigonid. In M_2 , however, the trigonid was wider than the talonid in only 28 of 57 cases. In one instance, the widths of the two parts of the tooth were equal. In M_3 the trigonid is always wider than the talonid. As indicated in Table 7, the dimensional variability of the premolar series is somewhat greater than that for the molar series with the exception of the length of M_3 .

Tayassu pecari
Upper Dentition

Deciduous teeth: The deciduous upper dentition of *Tayassu pecari* is substantially like that of the more robust variants of *Dicotyles tajacu* with the qualification that the premolars are absolutely larger and, in detail, more complex. In dP² accessory conules are found along the posterior surface of the paracone and on the posterolingual half of the heel. In dP³ an accessory conule anterior to the protocone is well differentiated.

Permanent teeth: The first incisor (Pl. 3) is essentially like that of *Dicotyles* except for being larger and stouter. The second incisor of *Tayassu* resembles that of certain members of *Dicotyles* in which the tip of the tooth is recurved so that it lies over the lingual portion of the crown rather than over the labial half of the tooth (see Tables 9, 10 for dimensions).

The second premolar (Pls. 3, 7, Fig. 8) of *Tayassu* generally resembles that of *Dicotyles* and is subject to about the same sorts of variation. In some specimens the anterior tip may be considerably narrower than the posterior portion, but in others the anterior end of the tooth is essentially blunt. In no case, however, was an increase in the height of the protocone and paracone observed to approach the relative elevation of these cusps in certain individuals of *Dicotyles*. The dimensions of the total sample for P² are given in Table 11. Individually, P² is neither longer nor wider than P³ (50 observations).

The third premolar is larger, generally more complexly wrinkled than in *Dicotyles*, but the general orientation of the cusps is about the same. In most cases the hypoconid is strongly developed from the lingual cingulum, but in some specimens it is reduced. The presence of a posterolabial cingular conule was often noted. See Table 11 for a summary of the dimensions of P³. In only one of 50 instances was P³ noted to be longer than the adjacent P⁴; P³ was uniformly narrower than P⁴.

The fourth premolar is larger than the third and generally more molariform; the hypoconid is more uniformly developed. In detail, the enamel surface is more finely crenulate than in *Dicotyles*. A summary of the dimensions of P⁴ is given in Table 11. In contrast to *Dicotyles* a survey of 50 individuals revealed only one case where P⁴ was wider than M¹ and none where P⁴ was longer. In one instance, the width of P⁴ equalled that of M¹.

The upper molars of *Tayassu* are generally constructed as in *Dicotyles*, but are larger and were often observed to have a strong continuous labial cingulum. In some cases, the metaconule was emphasized and elongated anterolabially. M³ was observed to

be extremely short in a few cases, a condition not usually found in *Dicotyles*. The dimensions of the upper molars are summarized in Table 11. In only one case out of 50 was M¹ found to be longer than M². The width of M¹ was never seen to be greater than for M². M² was longer than M³ in only four of 48 cases, and wider in 43 cases; the two teeth were equally wide in only one instance.

Lower Dentition

Deciduous teeth: The deciduous incisors and canines of *Tayassu* are not conspicuously different from those of *Dicotyles*, other than in terms of size.

Tayassu differs from *Dicotyles* in the more conspicuously bifid main cuspid and broader, more complex heel of dP₂. In similar fashion, the crown of dP₃ is more complex than in the collared peccary, and in addition, the tooth is broader and relatively shorter in *Tayassu* and the accessory conulids tend to be more distinctly developed. Other than in actual size and in the detailed complexity of the enamel surface, dP₄ of *Tayassu* is not markedly different from that of *Dicotyles*.

Permanent teeth: The permanent lower incisors (Pls. 5, 6) of *Tayassu* are small relative to the size of the mandible. As in the case of the upper canines, their lower counterparts are more robust, but relatively lower crowned than in *Dicotyles*. The dimensions of the lower incisors and canines are given in Tables 9 and 10.

As in the case of its deciduous predecessor, the permanent P₂ of *Tayassu* differs from comparable teeth in *Dicotyles* by the conspicuously bifid nature of its main cuspid (Pl. 6, Fig. 5). Also, as seen in the deciduous dentition, P₃ and P₄ of *Tayassu* are less hypsodont than in *Dicotyles*. In particular, the anterior conulids and other accessory conulids of the premolars of *Tayassu* are less prominent than in *Dicotyles*. Otherwise, the permanent cheek tooth dentitions of both genera are substantially similar. As mentioned previously both upper and lower cheek tooth series are set relatively closer together in *Tayassu* than in *Dicotyles*. Dimensions of the lower cheek teeth of *Tayassu* are given in Table 13. In general, the sample shows less variability in tooth dimensions than does that of *Dicotyles* (Table 7); this is particularly evident in the case of the premolars. Overlap in dimensions occurs throughout the series when the total sample for *Tayassu* is considered. Within individual specimens, however, the following relations apply. In 50 individuals $P_2 < P_3$, $P_3 < P_4$, $P_4 < M_1$, and $M_1 < M_2$. In all cases, M₂ was also shorter than M₃, but in only 14 instances was M₂ narrower than M₃. In two cases the widths of the two teeth were equal.

Some of the more pertinent variations observed in the cheek teeth of *Tayassu* include: P₂, non-bifurcate main cuspid, reduction in width relative to that of the molars; P₃, reduction of the small conulid along the posterior midline of the main cuspid, increase in the width of the heel, development of two transverse lophids on the heel; P₄, enlargement of the middle conulid on the heel to a longitudinally elongate lophid with concomitant reduction of the single conulid usually present between the trigonid and the rest of the talonid cuspids, increase in the width of the heel; M₁-M₃, increase in the relative width of the teeth and simplification of their enamel patterns by means of a decrease in the surface crenulations and commissures, posterior prolongation and extreme tapering of M₃. In general the dentition of *Tayassu* is not as variable as that of *Dicotyles*. While the rather wide range of dental variation in *Dicotyles* hinders the development of a clear-cut statement of the differences between the former genus and that of *Tayassu*, it would seem that on the whole, P₄ of the collared peccary is higher crowned relative to M₁ than in the white lipped peccary, and, further, that in the former the height of the trigonid relative to the height of the talonid of P₄ is greater than in *Tayassu*. In both genera P₄ erupts after M₂ and before M₃. Another subtle, but generally useful, distinction between *Dicotyles* and *Tayassu* is the generally sharper, more steeply sided cusps of teeth in both the upper and lower dentitions of *Dicotyles*. In *Tayassu*, the sides of the paracone, metacone, protoconid and hypoconid in particular, usually

slope gradually rather than abruptly from base to tip at a moderate, rather than steep, angle and the bases of these pairs of cusps tend to be more closely appressed to each other at the transverse valley.

The dental dimensions for the measured sample of *Tayassu pecari* usually overlap the ranges of the analogous dimensions for *Dicotyles tajacu* (compare Tables 3, 4, 5 and 7 with Tables 9, 10, 11 and 13). In some (e.g., width of I¹, width of I², length of I₁, and width of both the upper and lower canines) the degree of overlap is exceptionally large. Those dimensions in which the range of overlap is rather small include: length of P₂, width of P⁴, width of P₄, length of M¹, width of M², and width of M³. Dimensions in which no overlap is observed between the two samples are: length and width of M₁, length of M₂, and width of M₃. Comparison of the mean values of the dental dimensions indicates that the teeth of *Dicotyles tajacu* are usually between 10 and 20 per cent smaller than those of *Tayassu pecari*. Exceptions to this include: width of P² (*Dicotyles* is 22 per cent smaller than *Tayassu*), width of M³ (*Dicotyles* is 22 per cent narrower), width of C¹ (*Dicotyles* is three per cent smaller), width of M₁ (*Dicotyles* is 22 per cent narrower), width of M₂ (*Dicotyles* is 22 per cent narrower), and width of M₃ (*Dicotyles* is 24 per cent narrower). Thus, while many dental dimensions of the *Tayassu* sample might represent an allomorphic increase relative to *Dicotyles*, some, e.g., the dimensions of the canines, do not.

SUMMARY OF THE SALIENT DIFFERENCES BETWEEN DICOTYLES AND TAYASSU

Dicotyles tajacu

1. Cranium relatively low, wide and short.
2. Rostrum excavated above and anterior to infraorbital foramen; posterior border of canine buttress well defined.
3. Narial notch broad posteriorly.
4. Dorsal surface of rostrum generally narrow, convex.
5. Supraorbital-nasal canals converge markedly anteriorly, then diverge; canals well defined anteriorly.
6. Canine buttress large.
7. Buccinator fossa faces laterally, extends back to above M¹ or M².
8. Combined width of incisive foramina nearly one-half of the total width of the rostrum at I².
9. Palatal surface is rugose with subsidiary palatal

Tayassu pecari

1. Cranium relatively high, narrow and elongate.
2. Rostrum expanded ventrolaterally anterior to infraorbital foramen; posterior border of canine buttress not as well defined.
3. Narial notch acuminate posteriorly.
4. Dorsal surface of rostrum generally broad, relatively flat.
5. Supraorbital-nasal canals do not converge markedly anteriorly; canals not well defined anteriorly.
6. Canine buttress small.
7. Buccinator muscles do not originate in a fossa; attachment area faces ventrally below swollen maxillary sinus, extends back above P⁴.
8. Combined width of incisive foramina only about one-third of the total width of the rostrum at I².
9. Palatal surface is generally smooth; median keel

- foramina and a persistent median keel; palatal surface between the last molars is generally flat, or with only a slight, narrow, depression.
10. Width of the nasals is restricted between the premaxillaries.
 11. Fronto-parietal suture does not project markedly anteriorly near midline.
 12. Maxillo-frontal suture curves posteroventrally.
 13. Maxillo-jugal contact curves posterodorsally.
 14. Lateral surface of the jugal is excavated; the bone flares outward below the orbit.
 15. Height of the zygomatic arch posterior to the postorbital process is considerably less than that anterior to the process.
 16. Site of origin of *M. masseter lateralis profundus* on the ventral side of the jugal is moderately expanded anteriorly and faces ventrally.
 17. Site of origin of depressor snout muscles, below the facial crest, is shallow and is usually only slightly above the level of the origin of the masseteric muscles.
 18. Facial crest is smoothly continuous with the zygomatic crest.
 19. Infraorbital foramen lies above P^4 or M^1 and has a subcircular cross section.
 20. Pterygoid surface of the alisphenoid is relatively narrow.
 21. Basilar eminences are generally elongate, spindle shaped.
 22. Diastema is short, less than the length from P^2 to P^4 .
 23. Mandibular profile is sharply concave below the canines; the incisors project more anteriorly.
 24. Postdigastric sulcus is elongate, lies below M_2 to beyond M_3 .
 25. Digastric fossa is relatively shallow.
 26. Ascending ramus rises well behind M_3 .
 27. Angle of the mandible is slightly inflected.
 28. Tooth rows are relatively far apart; teeth are smaller, canines are slenderer and tend to be more elongate; cusps of the teeth are sharper; P_4 is higher crowned than M_1 .
 29. Overall size smaller.
- is absent; palatal surface between the last molars bears an elongate, ovoid moderately deep sulcus.
10. Width of the nasals is not restricted between the premaxillaries.
 11. Fronto-parietal suture projects markedly anteriorly near midline.
 12. Maxillo-frontal suture passes vertically.
 13. Maxillo-jugal contact is angulate, shaped as an inverted L.
 14. Lateral surface of the jugal is flat and not flared outward.
 15. Height of the zygomatic arch posterior to the postorbital process is nearly the same as that anterior to the process.
 16. Site of origin of *M. masseter lateralis profundus* on the ventral side of the jugal is broadly expanded anteriorly and faces ventrolaterally.
 17. Site of origin of depressor snout muscles is a deep pocket which lies considerably dorsal to the origin of the masseteric muscles.
 18. Facial crest diverges sharply upward from the zygomatic crest.
 19. Infraorbital foramen lies above P^4 or M^1 and has a flat, slit-like cross section.
 20. Pterygoid surface of the alisphenoid is broad.
 21. Basilar eminences are poorly distinguishable from each other, and are not linear.
 22. Diastema is long, equal to or slightly longer than the length from P^2 to P^4 .
 23. Mandibular profile below the canines is generally smoothly convex; the incisors project more dorsally.
 24. Postdigastric sulcus is shorter, lies below M_3 only.
 25. Digastric fossa is relatively deeper, with the adjacent ventral edge of the mandible produced inward.
 26. Ascending ramus passes by the rear half of M_3 .
 27. Angle of the mandible is not inflected.
 28. Tooth rows are relatively closer together; teeth are larger, canines are stouter and less elongate; cusps of the teeth are blunter, broader; height of P_4 is about equal to that of M_1 .
 29. Overall size larger.

THE ANCESTRY OF DICOTYLES AND TAYASSU

Although various inferences as to the habits of the North American fossil peccaries of Quaternary and late Tertiary age have been drawn from observations on the living species, it is intriguing that no close

relative of, for example, *Dicotyles tajacu*, has yet been found in the late Cenozoic fossil record of this continent. The pioneer investigations in paleontology by Leidy, Cope, Marsh and others resulted in the naming of a number of Tertiary "species" of *Dicotyles*, but these have since become relegated to

such genera as *Cynorca*, *Mylohyus*, *Platygonus* and *Prosthennops*. Although Pleistocene remains probably referable to one or the other of the Recent genera have been found in South America (Rusconi, 1931), species names have not been formally applied. *Dicotyles traunmülleri* Spillman, 1949, from the late Pliocene of Peru may be a valid species, but it is known from a proximal fragment of a humerus and a worn out left upper third molar. At first glance, much of the fossil record seems to be of little use in deciphering the past history of the Recent genera. The primary problem to be investigated, then, is: What paleontological evidence can be brought to bear on the question as to whether or not the living peccaries constitute valid genera?

As pointed out above, the major differences between the living genera of peccaries are found largely in their crania, the teeth being distinctive mainly in a subtle way. Furthermore, the occipital and temporal regions of the two forms do not differ appreciably although the post-dental portion of the cranium of *Tayassu* is shorter relative to its dental portion than in *Dicotyles*. In general, *Dicotyles tajacu* can be said to be a relatively short and heavily snouted peccary in which the site of the origin for the buccinator muscles is well expressed laterally, the masseteric muscles originate from an elongate, but relatively narrow, ventrally facing surface of the jugal and the site of origin of the depressor snout muscles occurs anterior to, but at about the same level as that of M. masseter. On the other hand, *Tayassu pecari* may be roughly characterized as a moderately long and slender snouted peccary with a ventral rather than lateral orientation of the attachment area for M. buccinator, an elongate but broad, ventrolaterally facing site of origin for M. masseter which lies relatively well below that of the depressor snout muscles.

Outside of the possibility, based on the increased hypsodonty of their premolar dentition, that some more northern races of *Dicotyles* are possibly less omnivorous than the individuals of *Tayassu* seem to be, it is difficult to correlate the morphological differences just summarized with any drastic behavioral differences. Whatever the mechanical and behavioral differences may be, however, it seems relatively certain that the above two suites of characters reflect the derivation of *Dicotyles* and *Tayassu* along somewhat different adaptive zones. The fossil record indicates further that two such adaptive zones extend as discrete evolutionary fields as far back as early Pliocene time.

In the following section the broader aspects of various late Tertiary tayassuid generic lineages will be discussed. A more detailed investigation of these lineages at the specific level will be the subject of

future work. Because it seems likely that the content of such established generic names as *Platygonus* and *Prosthennops* will be altered as a result of ensuing work, mention of a particular species of, for example, *Prosthennops*, should not be construed as binding on any other of the currently known species of the genus.

In *Prosthennops niobrarensis* (early Pliocene or possibly late Miocene of Nebraska) we find an animal with a moderately long, slender snout, small canine buttresses and, more importantly, an elongate, flat ventrolaterally facing surface on the ventral aspect of the zygomatic arch similar to that in *Tayassu*. The temporal region of the Nebraska fossil is relatively short and the post-canine diastema is about as long as the premolar dentition, as in *Tayassu*. On the other hand, the maxillary sinus is not swollen, so that while a strong buccinator fossa is not developed, the presumed site of origin for the buccinator muscles faces laterally, as in *Dicotyles*. Further discussion of the other species of *Prosthennops*, some of which are obviously too specialized to be of interest here (*P. crassigenis* Gidley, 1904) or are known chiefly from dental evidence, is beyond the scope of this report. It is sufficient for present purposes to indicate that, broadly speaking, *Prosthennops niobrarensis* is a suitable ancestral prototype of *Tayassu*. Other peccaries with crania of the same basic character as that summarized for *P. niobrarensis* are found in *Mylohyus nasutus* (Leidy, 1868) (see Lundelius, 1960) from the later Pleistocene of North America and in *Platygonus (Brasili-choerus) stenocephalus* (Rusconi, 1931, pp. 160-163, and Winge, 1906, pl. 6) from the latest Pleistocene or earliest Recent of South America. The three species just mentioned not only share most of the features enumerated for *P. niobrarensis* but also have a broad depression just dorsal to the anterior end of the zygomatic arch and anterior to the orbit. It seems likely that this depression contained the origin of the depressor snout muscles. The depression is shallow in *P. niobrarensis* but in both *Mylohyus* and *Platygonus (B.) stenocephalus* it is backed by a distinct ridge. To judge from the illustrations in Lundelius (1960) this ridge is oriented at a moderately shallow angle and extends anterodorsally in *Mylohyus nasutus*. In *Platygonus (B.) stenocephalus*, however, the ridge is aligned nearly vertically, even more steeply than in *Tayassu*. Available information on the dentition of the South American genus is rather scanty. It appears that the type specimen was aberrant to the extent that a supernumary tooth is present between M¹ and M² on each side of the palate. Although the crowns of the teeth illustrated by Winge (1906, pl. 6) are rather worn (particularly the lowers) the dentition of *Platygonus (B.) steno-*

cephalus seems to be less specialized than that of *Mylohyus*, and thus more like the cheek teeth of *Tayassu*. In spite of the various differences shown by the Brazilian genus, such as its larger size, greater elongation of the snout and the positioning of the glenoid fossa directly beneath the orbits, there can be little doubt that this animal descended from the same general prototype as produced *Tayassu pecari*. The latter appears to be more generalized in terms of its rather bunodont dentition, shorter snout, shorter post-canine diastema and more robust incisors than either *Mylohyus* or the Brazilian genus (but note that the incisors of the latter are not known). On the other hand, *Tayassu* differs from these, and all other currently known genera of peccaries in the conspicuous expansion of its maxillary sinus. The fact remains, however, that *Tayassu*, *Mylohyus* and the Brazilian peccary seem to be more closely related to each other than to any other fossil representative, and that the ultimate ancestry of all three probably passed through a stage similar to *Prosthennops niobrarensis*.

The determination of the paleontological associates of *Dicotyles tajacu* is not as straightforward as in the case of *Tayassu*. But, using the broad characterization of the collared peccary as set out at the beginning of this section, it can be seen that there is a close basic resemblance between the Recent genus and various North American species of *Platygonus*. In particular, the cranium which Skinner (1942) referred to *Platygonus alemanii* Dugès, 1887 shows a number of basic similarities to *Dicotyles tajacu*. These include the relatively deep, moderately short snout, the ventrally facing site of origin for M. masseter lateralis profundus, the lip-like lateral boundary of this attachment area, the straight, anteriorly directed facial crest and the well developed horizontal bony ridge defining the dorsal limit of the buccinator fossa. Although it is rather short, the facial crest extends somewhat anteroventrally, in marked contrast to the sharply anterodorsal configuration noted in *Tayassu* and *Platygonus (Brasili-choerus) stenocephalus*. In a recent review Slaughter (1966) suggests that the number of late Pleistocene species of *Platygonus* proposed in the literature may be reduced to *Platygonus compressus* Le Conte, 1848, *Platygonus vetus* Leidy, 1882, and *Platygonus cumberlandensis* Gidley, 1920. *P. compressus* includes *Hyops depressifrons* Le Conte, 1848, *Dicotyles costatus* Le Conte, 1848, *Euchoerus macrops* Leidy, 1853, *Platygonus leptorhinus* Williston, 1894, and probably *P. alemanii* Dugès, 1887. Simpson (1949) indicated that *Platygonus setiger* Hay, 1920, and *Platygonus francisi* Hay, 1920, are also synonyms of *P. compressus* and that *Protochoerus prismaticus* Le Conte, 1848, is a *nomen vanum*.

Platygonus cumberlandensis includes *P. intermedius* Gidley, 1920, and is characterized as having a long, slender snout, relatively long postcanine diastema, broadly flaring zygomatic arches, and a glenoid fossa which is usually positioned below the level of the occlusal plane.

Inasmuch as the morphological summary given above for *P. alemanii* could apply equally well to *P. compressus* (see Simpson, 1949, figs. 6, 7), the latter can be taken to represent peccaries which differ from *P. cumberlandensis* and resemble *Dicotyles tajacu* having a shorter, deeper snout, less strongly flaring zygomatic arches, shorter postcanine diastemata, and a higher position of the glenoid fossa. In this regard, *P. compressus* may be said to represent a less specialized level of organization than does *P. cumberlandensis*. The type cranium of *P. vetus* unfortunately does not portray many of the features cited above, but to judge from the low diastema-cheek tooth index (54) it might fall into the short snouted group, being at least a collateral species relative to *P. compressus*. Slaughter (1966) cites the large size of the dentition of *P. vetus* as setting it apart from the other two species of the genus, noting that it might be more closely allied to *P. cumberlandensis*. My interpretation, based on meager information as to the probable construction of the cranium, differs from his, but resolution of this point is not critical to the present study.

In view of the similarly low (ca. 40) diastema-cheek tooth index calculated

$$\frac{\text{length, post-canine diastema}}{\text{length, cheek tooth series}} \times 100$$

for *Platygonus texanus* Gidley, 1903, this early Pleistocene form may also be a member of the lineage leading toward *P. compressus*. The material preserved for *Platygonus bicalcaratus* Cope, 1893, from the early Pleistocene of Texas, is insufficient for evaluation in the present context. I have not seen the actual material of *Platygonus pearcei* Gazin, 1938, from the late Pliocene Hagerman fauna of Idaho, but to judge from the illustrations (Gazin, 1938, Fig. 2) this is a long-snouted species with widely flaring zygomatic arches and is probably a member of the lineage leading toward *P. cumberlandensis*.

This preliminary survey suggests that the genus *Platygonus* contains at least two major lines of descent in North America; that leading toward *P. cumberlandensis* is traceable into the late Pliocene while the *P. compressus* stem may carry back as least as far as the early Pleistocene on present evidence. Of the two, the *P. compressus* group seems to be the more conservative and thus shows closest affinity with *Dicotyles tajacu*. The earliest currently known record for the direct ancestry of the latter

may be represented by *D. traunmülleri* from the late Pliocene of Peru. A South American branch of *Platygonus* is found in *Platygonus* (*Parachoerus*) *carlesi* which, along with a derivative subspecies, is known from deposits of middle to latest Pleistocene age (Rusconi, 1931, pp. 150-159, 231-238, Pls. 3-6, 16-18 Figs. 26, 31, 32). From Rusconi's description and figures, the cranium of *Platygonus* (*P.*) *carlesi* resembles that of *Dicotyles* in the following points: anterior constriction of the supraorbital-nasal canals, decrease in vertical height of the zygomatic arch posterior to the postglenoid process, the excavation of the lateral surface of the maxillary posterior to the canines and anterior to the zygomatic arch, the smooth continuation of the facial crest at a shallow angle anterodorsally from the zygomatic crest, the narrow, elongate, ventrally facing site of origin of the masseteric muscles, the slightly rather than strongly curved profile of the ventral edge of the zygomatic crest as seen in lateral view, the strong canine buttresses and the absence of an expanded maxillary sinus. In most of these points, the Argentine genus also resembles the North American species of *Platygonus*, but almost all the characters listed constitute differences when compared with *Tayassu*, *Mylohyus*, *Platygonus* (*Brasiliochoerus*) *stenocephalus* and *Prosthennops niobrarensis*. Continued association of *Brasiliochoerus stenocephalus* with *Platygonus*, which is not only misleading but seems also to be inconsistent with the evidence summarized in this discussion, should be rectified at some future time.

A more detailed consideration of the affinities of the various South American peccaries will be undertaken at a later date, but for the present it is sufficient to note that *Platygonus* (*Parachoerus*) *carlesi*, *Dicotyles tajacu* and the North American species of *Platygonus* are more closely related to each other than either is to any of the other genera and species discussed herein. Although the crowns of the teeth of *Platygonus* (*P.*) *carlesi* are worn down, the dentition of a later subspecies, *Platygonus* (*P.*) *carlesi wagneri* (Rusconi, 1931, Pls. 16-18) seems to be somewhat less hypsodont and zygodont than in the North American species of *Platygonus*. In these terms, the dentition of the Argentine subspecies approaches the condition of some undescribed early Pliocene peccaries in the Frick Collection of the American Museum of Natural History. The cheek teeth of the latter specimens can be readily separated from the teeth of contemporaneous representatives of *Prosthennops* and, at the same time, are suitably constructed to serve, in a broad way, as the ancestral prototype of *Dicotyles* and the various species of *Platygonus*.

Dentally, at least, *Dicotyles* seems to be a remnant

of an earlier level of organization and, except for the strong facial crest, its cranium is more generalized than that of *Platygonus*. Cranial material of the pertinent specimens in the Frick Collection is unfortunately not preserved. The cranium of *Dyseohyus fricki* (late Miocene of California) is substantially like that of *Prosthennops niobrarensis* and is thus an unsuitable ancestor for *Dicotyles* unless substantial modifications, for which there is no current evidence, took place in the intervening steps. The other potential ancestor of *Dicotyles*, *Cynorca* (Miocene of various North American localities), is known mainly by its dentition which is somewhat more primitive, particularly in the degree of molarization of the premolars, than that of *Dyseohyus*. Discovery of cranial material of *Cynorca*, which is strategically placed in time and space, might cast new light on the origin of *Dicotyles*.

The prevailing uncertainties notwithstanding, the proposal that *Dicotyles tajacu* and *Tayassu pecari* are members of independent, long-lived lineages seems to be corroborated by the available fossil evidence; morphologically and paleontologically, the separation of these two peccaries at the generic level seems to be not only eminently reasonable, but warranted by the facts and inferences presented herein.

In summary, *Cynorca* and *Dyseohyus* are the only known genera which are suitable ancestors for the Pliocene, Pleistocene and Recent peccaries. The lineage which ultimately produced *Tayassu pecari* is broadly associated with *Mylohyus* and "*Platygonus*" (*Brasiliochoerus*) *stenocephalus*. The common line of descent for these three peccaries can probably be traced through *Prosthennops niobrarensis* and thence to *Dyseohyus*. The oldest known records of *Tayassu* are found in the late Pleistocene or early Recent of South America and direct fore-runners of this genus certainly have not yet come to light in Pliocene or Pleistocene deposits of North America. The probability that *Tayassu* underwent most of its evolution in Central and South America is relatively great.

A similar statement can be made for *Dicotyles*, whose earliest known occurrence is in the late Pliocene of Peru. The point in space and time when *Dicotyles* diverged from its phyletic associate, *Platygonus*, cannot yet be documented and inferences as to the ultimate origin of the *Dicotyles* — *Platygonus* branch of the peccary family tree cannot be as readily made as for *Tayassu* and its associates.

Both the white lipped and collared peccaries possess a relatively large number of conservative characters and hence are less divergent, than the other more specialized members of their respective lineages, from the basic morphological level repre-

sented by *Dyseohyus* and *Cynorca*. The living peccaries have thus outlasted their more progressive relatives. On the other hand, the morphological proximity of *Dicotyles* and *Tayassu* to the ancestral fount of the later Tertiary and Quaternary Tayassuidae has tended to obscure the fact that their adaptive separation has indeed been of a duration and magnitude which warrants generic distinction.

CONCLUSIONS

The nomenclature of the modern peccaries has been confused for many years. The following chronologic summary (Table 14) indicates the progression of the various names. Since the names of Frisch (1775) do not apply to zoological nomenclature by reason of their being non-Linnaean (see Hershkovitz, 1948) the earliest valid generic name for any peccary seems to be *Tayassu* Fischer, 1814. The genotypic species for this genus is clearly *T. pecari*, the white lipped peccary. All later names for the white lipped species are pre-empted by, and are synonymous with, this binomial and, according to the conclusions of the current study, the genus *Tayassu* is monotypic, as far as the Recent fauna is concerned.

Fischer (1814) also proposed the name *Tayassu patira* for the collared peccary, but as indicated above, the genus *Tayassu* is not available for this usage and the species *T. patira* is predated by *Sus tajacu* Linnaeus, 1758.

The next available name for the collared peccary is *Dicotyles* Cuvier, 1817. The usage of the name *Dicotyles* has had a complex history, most of the

difficulty seeming to have resulted by the "designation" by Gray (1868) of *D. labiatus* (white lipped peccary) as the genotypic species. Thus, *Dicotyles* came to be considered as synonymous with *Tayassu* Fischer, 1814, although the former name was held to be esthetically preferable by a number of workers and was utilized by many North American paleontologists and neontologists in the late 19th and early 20th centuries. At one time, a proposal was put before the International Commission on Zoological Nomenclature to have the rules suspended in favor of *Dicotyles*, but this was turned down (opinion 90; see Schenk and McMasters, 1948, p. 58). Now that the living peccaries are treated as separate genera, *Dicotyles* should again become available for evaluation. From Cuvier's text (1817, pp. 237-238) *D. torquatus* is clearly the genotypic species of *Dicotyles* and refers to the collared peccary. *D. torquatus* not only has page priority over *D. labiatus* (Cuvier's name for the white lipped peccary), but is more thoroughly diagnosed than the latter and seems to have been central to Cuvier's concept of the genus.

There can be little doubt that *Dicotyles torquatus* refers to a different species of peccary than does *Tayassu pecari*. In light of the current study, the two species also represent distinct genera. *Tayassu pecari* Fischer, 1814, refers to the white lipped peccary. The collared peccary would be designated as *Dicotyles torquatus* Cuvier, 1817, were it not for the fact that Cuvier's specific name, but not his generic name is pre-dated by *Tayassu patira* Fischer, 1814, and *Sus tajacu* Linnaeus, 1758. The collared peccary must be known, therefore, as *Dicotyles tajacu* (Linnaeus, 1758).

NOTE ADDED IN PROOF

During the time this paper was in page proof, Mr. William A. Low, Dept. Zoology, Univ. British Columbia, brought to my attention a paper by Hershkovitz (P., 1963. Proc. Biol. Soc. Wash., 76: 85-88) in which Link (D.H.F., 1795. Beiträge zur Naturgeschichte. Rostock und Leipzig, 2: 1-126) is given credit for *Tayassu pecari*, the name for the white lipped peccary. I have not been able to obtain a copy of Link's article as yet and have not been able to make a decision on this point. Although this nomenclatural technicality should be pursued further, it alters neither the broader conclusions set out above nor the name of the collared peccary.

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PLATE 1

Dicotyles tajacu torvus ♂. A.M.N.H. (M.) No. 92838, adult cranium.
1. Dorsal view. 2. Lateral view. 3. Ventral view. Approximately X $\frac{1}{2}$



PLATE 2

Dicotyles tajacu angulatus ♀. A.M.N.H. (M.) No. 22764, adult cranium.
1. Dorsal view. 2. Lateral view. 3. Ventral view. Approximately X $\frac{1}{2}$



PLATE 3

Tayassu pecari beebei -, A.M.N.H. (M.) No. 142981, adult cranium.

1. Dorsal view. 2. Lateral view. 3. Ventral view. X $\frac{1}{2}$

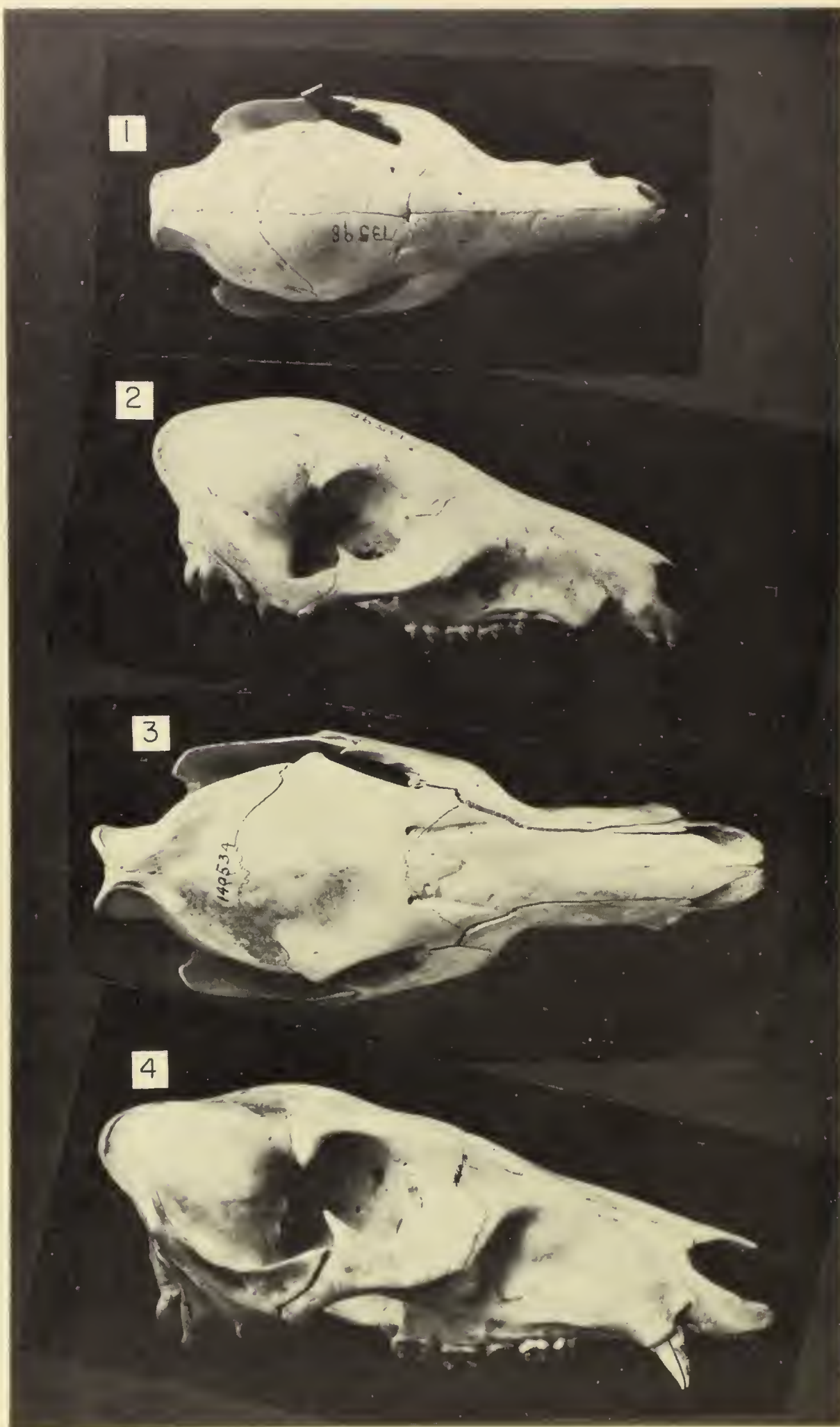


PLATE 4

1, 2. *Dicotyles tajacu torvus* -. A.M.N.H. (M.) No. 73598, immature cranium with dI^{1-2} , dC^1 , dP^{2-4} , M^1 . 1. Dorsal view. 2. Lateral view. 3, 4. *Tayassu pecari beebei* -. A.M.N.H. (M.) No. 140534, subadult cranium with canine and P^2-M^2 . 3. Dorsal view. 4. Lateral view. X $\frac{1}{2}$

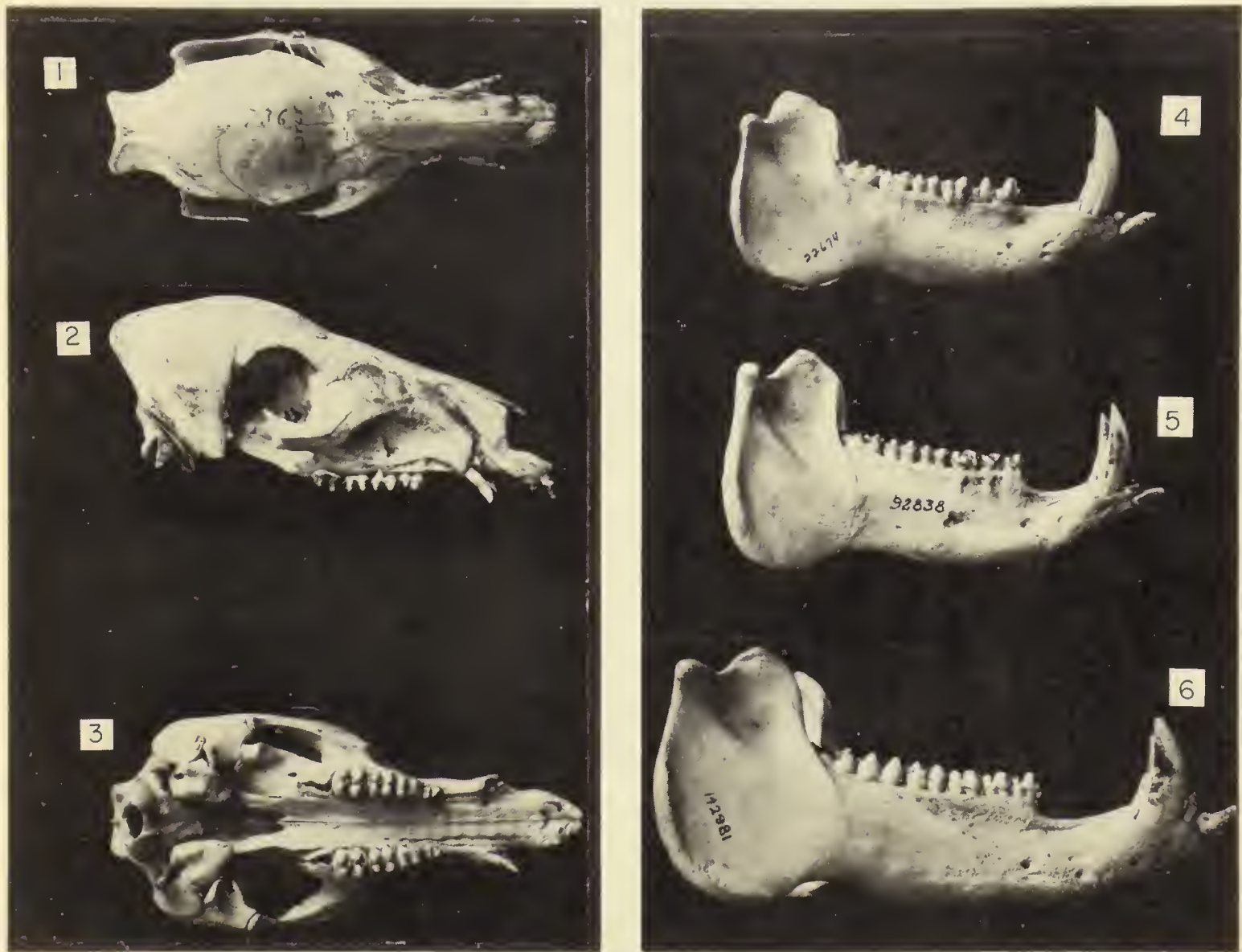


PLATE 5

1, 2, 4. *Dicotyles tajacu angulatus*. 1, 2. A.M.N.H. (M.) No. 23868. 1. Dorsal view of immature cranium. 2. Lateral view of immature cranium. 4. A.M.N.H. (M.) No. 22674 ♀. Right mandible. Lateral view. 3, 5. *Dicotyles tajacu torvus*. 3. A.M.N.H. (M.) No. 73598 -. Ventral view of immature cranium with dI¹⁻², dC¹, dP²⁻⁴, M¹. 5. A.M.N.H. (M.) No. 92838 ♂. Adult mandible, lateral view. 6. *Tayassu pecari beebei* -. A.M.N.H. (M.) No. 142981. Adult mandible, lateral view. All X 1/3.



PLATE 6

1. *Dicotyles tajacu angulatus* ♀. A.M.N.H. (M.) No. 22674. 2, 4, 5. *Tayassu pecari beebei* -. A.M.N.H. (M.) No. 142981. 3. *Dicotyles tajacu torvus* ♂. A.M.N.H. (M.) No. 92838. 1, 2. Adult mandibles. Ventral view. 3, 4. Adult mandibles. Occlusal view. 5. Right lower cheek teeth. Occlusal view. 1-4, X $\frac{1}{2}$. 5, X 1.

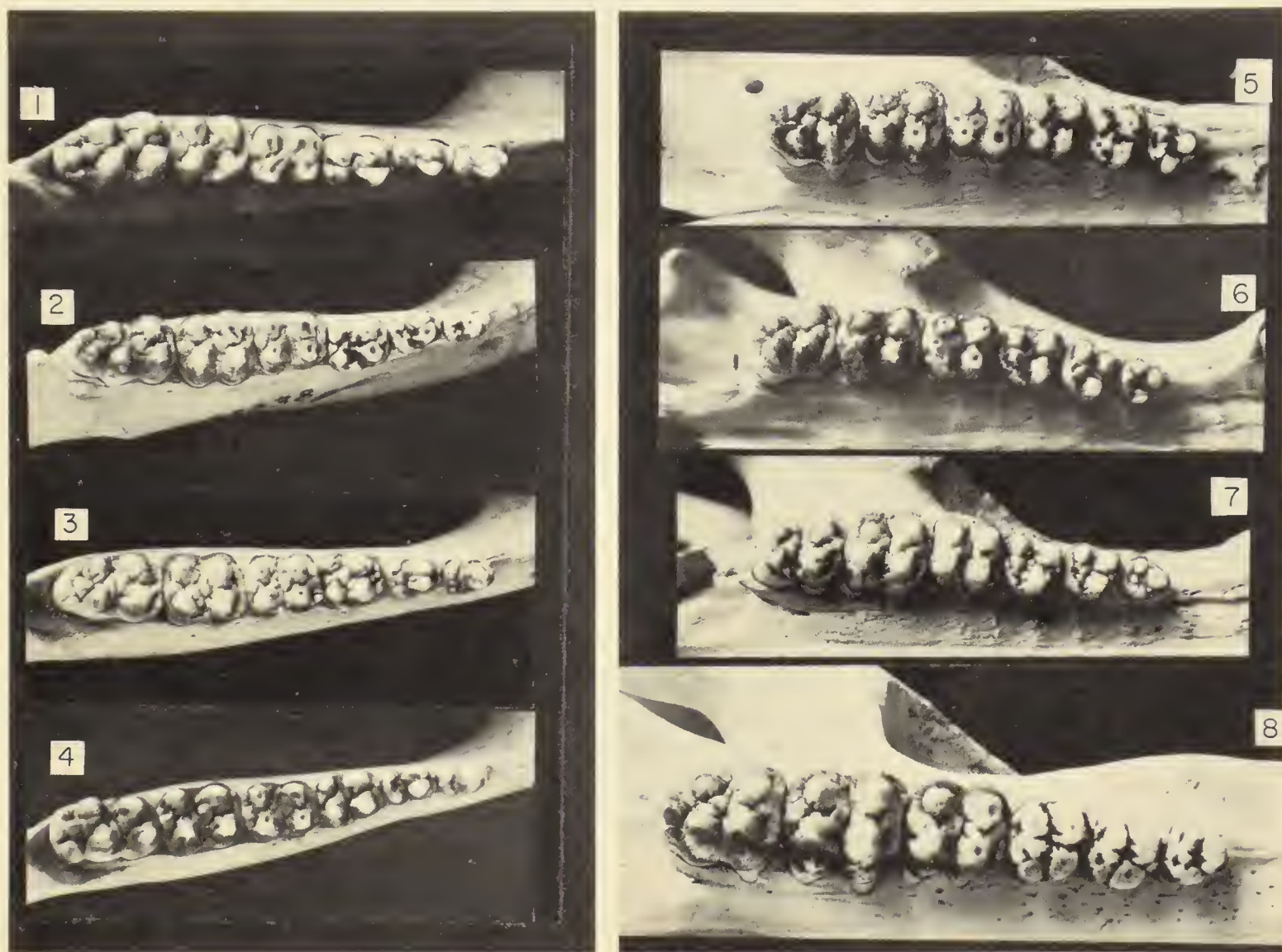


PLATE 7

1. *Dicotyles tajacu angulatus* ♀. A.M.N.H. (M.) No. 22764. 2-7. *Dicotyles tajacu torvus*. 2. A.M.N.H. (M.) No. 92838 ♂. 3. A.M.N.H. (M.) No. 98850 ♂. 4. A.M.N.H. (M.) No. 23531 -. Right lower cheek teeth. 5. A.M.N.H. (M.) No. 92838 ♂. 6. A.M.N.H. (M.) No. 23531 -. 7. A.M.N.H. (M.) No. 98550 ♂. 8. *Tayassu pecari beebei* -. A.M.N.H. (M.) No. 142981. Right upper cheek teeth. All X 5/6

TABLE 2. Cranial Measurements (in mm) of *Dicotyles tajacu*.

	N	OR	M	s	V
Length from the tip of I ¹ to the rear of the condyles	71	179.15-228.65	201.58± 1.16	9.73± 0.82	4.83± 0.41
Length, diastema from C ¹ to P ²	71	10.25- 24.75	18.28± 0.36	3.01± 0.25	16.48± 1.38
Width between the alveoli of P ²	71	14.65- 22.50	18.53± 0.21	1.74± 0.15	9.38± 0.79
Width between the alveoli of M ³	71	14.80- 22.00	18.22± 0.22	1.88± 0.16	10.32± 0.87
Least width of the rostrum	71	16.70- 37.20	31.60± 0.36	3.03± 0.25	9.57± 0.80
Height from the condyles to the nuchal crest	71	73.95- 91.60	81.63± 0.51	4.26± 0.36	5.22± 0.44
Breadth across the zygomatic arches	71	91.10-111.15	101.45± 0.52	4.40± 0.37	4.33± 0.36
Breadth between the postorbital processes of the frontals	71	63.70- 82.85	73.00± 0.49	4.11± 0.35	5.63± 0.47

TABLE 3. Measurements (in mm) of Incisors of *Dicotyles tajacu*.

	N	OR	M
I ¹			
Length	75	7.10-13.10	10.86
Width	76	6.30- 9.25	7.68
I ²			
Length	74	6.25- 9.55	7.86
Width	76	4.15- 6.15	5.19
I ₁			
Length	77	3.40- 5.75	4.39
Width	77	4.70- 7.10	6.15
I ₂			
Length	76	3.80- 5.70	4.66
Width	76	5.40- 7.80	6.51
I ₃			
Length	70	2.50- 6.65	4.48
Width	70	2.20- 4.35	3.18

TABLE 4. Measurements (in mm) of Canines of *Dicotyles tajacu*.

	N	OR	M	s	V
Upper canine					
Total sample					
Length	71	10.10-15.30	12.56±0.15	1.29±0.11	10.25±0.86
Width	71	6.20-10.75	8.55±0.12	1.06±0.09	12.44±1.04
Male individuals					
Length	9	11.25-14.30	12.70±0.33	0.99±0.23	7.80±1.84
Width	22	6.80-10.15	8.71±0.17	0.82±0.12	9.41±1.42
Female individuals					
Length	10	10.50-13.30	11.72±0.27	0.84±0.19	7.17±1.60
Width	17	7.50-10.75	8.27±0.19	0.80±0.14	7.37±1.26
Lower canine					
Total sample					
Length	71	8.55-13.90	10.91±0.15	1.29±0.11	11.42±1.00
Width	71	6.50-11.30	8.77±0.13	1.13±0.09	12.89±1.01
Male individuals					
Length	19	9.65-13.90	11.30±0.25	1.09±0.18	9.65±1.57
Width	21	6.55-11.00	8.93±0.25	1.14±0.18	12.78±1.97
Female individuals					
Length	17	9.10-13.20	10.41±0.24	1.05±0.18	10.09±1.73
Width	17	7.05-10.00	8.65±0.15	0.62±0.11	7.17±1.23

TABLE 5. Dimensions (in mm) of upper cheek teeth of *Dicotyles tajacu*.

	N	OR	M	s	V
Length, I ¹ -M ³	71	115.70-114.15	128.22±0.58	4.89±0.41	3.80±0.32
Length, P ² -M ³	71	56.25- 69.20	63.85±0.32	2.70±0.23	4.23±0.36
p ²					
Length	71	6.95- 9.70	8.30±0.07	0.56±0.05	6.77±0.57
Width	71	5.75- 9.05	7.38±0.08	0.68±0.06	9.22±0.77
p ³					
Length	71	8.00- 10.20	9.18±0.06	0.50±0.04	5.45±0.46
Width	71	7.35- 10.55	9.26±0.07	0.60±0.05	6.44±0.54
p ⁴					
Length	71	8.90- 11.50	10.10±0.07	0.63±0.05	6.23±0.52
Width	71	8.70- 11.75	10.57±0.08	0.68±0.06	6.43±0.54
M ¹					
Length	71	9.80- 12.85	11.57±0.07	0.62±0.05	5.39±0.45
Width	71	9.10- 13.00	10.97±0.08	0.63±0.05	5.79±0.49
M ²					
Length	71	11.10- 14.40	13.16±0.08	0.68±0.06	5.15±0.43
Width	71	10.05- 14.35	12.47±0.09	0.79±0.07	6.36±0.53
M ³					
Length	71	11.50- 16.50	13.95±0.11	0.95±0.08	6.83±0.57
Width	71	10.30- 13.20	11.76±0.08	0.66±0.06	5.60±0.47

TABLE 6. Dimensions (in mm) of the lower jaw of *Dicotyles tajacu*.

	N	OR	M	s	V
Length, I ₁ to rear of the condyles	71	147.25-188.60	161.98±0.94	7.93±0.67	4.89±0.41
Length, diastema from C ₁ to P ₂	71	17.60- 38.40	24.69±0.38	3.22±0.27	13.03±1.09
Depth, tip of coronoid process to ventral edge of angle	71	65.00- 83.10	75.25±0.51	4.29±0.36	5.71±0.48
Depth, below P ₂	71	26.10- 39.40	32.10±0.32	2.68±0.23	8.34±0.70
Depth, below M ₃	71	26.90- 39.80	33.71±0.33	2.77±0.23	8.23±0.69
Width, between P ₂ alveoli	71	17.15- 26.85	22.13±0.21	1.80±0.15	8.11±0.68
Width, between M ₃ alveoli	71	22.45- 32.15	27.01±0.24	2.04±0.17	7.55±0.63
Width, between the condyles	71	41.15- 55.35	48.97±0.33	2.79±0.23	5.69±0.48

TABLE 7. Measurements (in mm) of lower cheek teeth of *Dicotyles tajacu*.

	N	OR	M	s	V
Length, P ₂ -M ₃	71	61.50-76.05	69.49±0.35	2.93±0.25	4.22±0.35
P ₂					
Length	71	7.10- 8.95	8.05±0.06	0.51±0.04	6.35±0.53
Width	71	3.80- 5.45	4.67±0.05	0.42±0.04	8.92±0.75
P ₃					
Length	71	7.60-10.35	9.11±0.06	0.50±0.04	5.50±0.46
Width	71	5.15- 7.20	6.05±0.06	0.47±0.04	7.74±0.65
P ₄					
Length	71	9.00-12.40	10.66±0.08	0.67±0.06	6.26±0.53
Width	71	6.35- 9.95	8.65±0.07	0.61±0.05	7.03±0.59
M ₁					
Length	71	10.30-13.30	11.80±0.07	0.61±0.05	5.17±0.43
Width	71	8.00-10.80	9.68±0.07	0.56±0.05	5.80±0.49
M ₂					
Length	71	12.00-14.95	13.27±0.08	0.65±0.05	4.90±0.41
Width	71	9.75-13.00	11.37±0.08	0.69±0.06	6.03±0.51
M ₃					
Length	71	12.30-20.50	17.31±0.16	1.36±0.11	7.85±0.66
Width	71	9.45-12.40	10.87±0.08	0.71±0.06	6.53±0.55

TABLE 8. Cranial measurements (in mm) of *Tayassu pecari*.

	N	OR	M	s	V
Length from the tip of I ¹ to the rear of the condyles	41	223.80-269.85	234.12 ± 1.69	10.79 ± 1.15	4.44 ± 0.49
Length, diastema from C ¹ to P ²	41	20.05- 33.20	25.97 ± 0.50	3.21 ± 0.35	12.35 ± 1.36
Width between the alveoli of P ²	41	16.50- 25.30	20.70 ± 0.31	2.02 ± 0.22	9.74 ± 1.08
Width between the alveoli of M ³	41	13.95- 23.75	20.11 ± 0.34	2.12 ± 0.23	10.73 ± 1.18
Least width of the rostrum	41	46.90- 61.40	52.81 ± 0.44	2.82 ± 0.31	5.33 ± 0.59
Height from the condyles to the nuchal crest	41	92.20- 109.25	98.41 ± 0.66	4.23 ± 0.47	4.31 ± 0.47
Breadth across the zygomatic arches	41	105.65- 124.80	117.32 ± 0.78	4.99 ± 0.55	4.25 ± 0.47
Breadth between the postorbital processes of the frontals	41	84.70-100.15	91.63 ± 0.60	3.86 ± 0.43	4.21 ± 0.46

TABLE 9. Measurements (in mm) of Incisors of *Tayassu pecari*.

	N	OR	M
I ¹			
Length	40	9.55-14.75	11.46
Width	40	6.10- 9.90	7.40
I ²			
Length	38	8.15-12.20	9.47
Width	38	4.55- 7.00	5.41
I ₁			
Length	42	3.95- 5.80	4.92
Width	44	6.10- 8.75	6.98
I ₂			
Length	38	4.40- 7.00	5.40
Width	38	6.35- 9.20	7.39
I ₃			
Length	38	4.50- 7.65	5.95
Width	38	3.40- 5.00	4.10

TABLE 10. Measurements (in mm) of canines of *Tayassu pecari*.

	N	OR	M	s	V
Upper canine					
Total sample					
Length	41	11.10-17.90	15.08±0.23	1.48±0.16	9.83±1.08
Width	41	6.40-12.50	8.91±0.24	1.57±0.17	17.58±1.94
Male individuals					
Length	10	10.10-14.90	13.60±0.49	1.53±0.34	11.25±2.52
Width	10	7.35-10.45	8.54±0.26	0.83±0.19	9.72±2.17
Female individuals					
Length	12	10.80-15.45	13.38±0.47	1.61±0.32	12.03±2.41
Width	12	6.80- 9.85	8.26±0.25	0.86±0.17	10.41±2.08
Lower canine					
Total sample					
Length	41	10.55-16.25	13.03±0.20	1.31±0.14	10.05±1.11
Width	41	7.45-13.25	9.73±0.22	1.41±0.16	14.51±1.60
Male individuals					
Length	10	9.40-14.00	11.61±0.43	1.36±0.30	11.71±2.62
Width	10	7.55-10.90	9.14±0.35	1.09±0.24	11.93±2.67
Female individuals					
Length	14	9.10-14.25	9.10±0.38	1.44±0.28	13.13±2.48
Width	14	7.05-10.40	8.98±0.25	0.95±0.18	10.57±2.00

TABLE 11. Dimensions (in mm) of upper cheek teeth of *Tayassu pecari*.

	N	OR	M	s	V
Length, I ¹ -M ³	41	147.95-173.70	159.43±1.06	6.76±0.75	4.24±0.47
Length, P ² -M ³	41	70.00- 84.10	75.15±0.49	3.16±0.35	4.40±0.49
p ²					
Length	41	8.50- 11.50	9.87±0.10	0.65±0.07	6.62±0.73
Width	41	8.45- 10.55	9.41±0.08	0.52±0.06	5.54±0.61
p ³					
Length	41	9.80- 12.30	10.98±0.10	0.64±0.07	5.85±0.65
Width	41	9.90- 12.25	11.16±0.08	0.53±0.06	4.73±0.52
p ⁴					
Length	41	10.85- 13.45	12.00±0.09	0.56±0.06	4.68±0.52
Width	41	11.15- 13.80	12.43±0.08	0.51±0.06	4.13±0.46
M ¹					
Length	41	12.65- 16.00	14.47±0.11	0.71±0.08	4.88±0.54
Width	41	12.15- 15.60	13.55±0.12	0.78±0.09	5.76±0.64
M ²					
Length	41	11.95- 17.70	16.12±0.16	1.03±0.11	6.36±0.70
Width	41	14.00- 18.00	15.38±0.13	0.85±0.09	5.52±0.61
M ³					
Length	41	14.85- 19.30	17.28±0.14	0.89±0.10	5.15±0.57
Width	41	13.65- 19.65	14.97±0.16	1.01±0.11	6.72±0.74

TABLE 12. Dimensions (in mm) of the lower jaw of *Tayassu pecari*.

	N	OR	M	s	V
Length, I ₁ to rear of the condyles	41	180.00-217.85	196.84 ± 1.38	8.84 ± 0.98	4.49 ± 0.50
Length, diastema from C ₁ to P ₂	41	27.35- 41.80	33.68 ± 0.46	2.97 ± 0.33	8.82 ± 0.97
Depth, tip of coronoid process to ventral edge of angle	41	83.70-107.80	92.08 ± 0.91	5.85 ± 0.65	6.35 ± 0.70
Depth, below P ₂	41	30.90- 40.60	35.97 ± 0.35	2.24 ± 0.25	6.22 ± 0.69
Depth, below M ₃	41	34.80- 45.70	40.51 ± 0.38	2.45 ± 0.27	6.06 ± 0.67
Width, between P ₂ alveoli	41	21.45- 29.30	25.65 ± 0.25	1.59 ± 0.18	6.70 ± 0.68
Width, between M ₃ alveoli	41	20.50- 39.70	30.51 ± 0.42	2.71 ± 0.30	8.87 ± 0.98
Width, between the condyles	41	52.45- 63.45	57.96 ± 0.46	2.93 ± 0.32	5.05 ± 0.56

TABLE 13. Measurements (in mm) of lower cheek teeth of *Tayassu pecari*.

	N	OR	M	s	V
Length, P ₂ -M ₃	41	78.20-93.35	85.22 ± 0.52	3.37 ± 0.37	3.95 ± 0.44
P ₂ Length	41	8.75-10.60	9.70 ± 0.07	0.46 ± 0.05	4.68 ± 0.52
Width	41	4.95- 6.60	5.80 ± 0.06	0.37 ± 0.04	6.46 ± 0.71
P ₃ Length	41	9.55-12.10	10.89 ± 0.08	0.53 ± 0.06	4.88 ± 0.54
Width	41	6.45- 8.70	7.39 ± 0.07	0.44 ± 0.05	5.00 ± 0.66
P ₄ Length	41	11.70-14.00	12.88 ± 0.09	0.59 ± 0.07	4.59 ± 0.51
Width	41	9.20-12.65	10.64 ± 1.01	0.65 ± 0.07	6.08 ± 0.67
M ₁ Length	41	14.00-16.25	14.94 ± 0.97	0.62 ± 0.07	4.17 ± 0.46
Width	41	10.90-14.40	12.36 ± 1.22	0.79 ± 0.09	6.35 ± 0.70
M ₂ Length	41	15.15-18.35	16.50 ± 1.24	0.79 ± 0.09	4.81 ± 0.53
Width	41	12.35-16.60	14.58 ± 1.48	0.95 ± 0.10	6.50 ± 0.72
M ₃ Length	41	18.45-24.30	21.72 ± 1.88	1.20 ± 0.13	5.54 ± 0.61
Width	41	12.65-16.20	14.33 ± 1.34	0.86 ± 0.09	6.01 ± 0.66

TABLE 14. Summary of names commonly applied to the living peccaries

	White lipped Peccary	Collared Peccary
Linnaeus, 1758		<i>Sus tajacu</i>
Frisch, 1775		<i>Tagassu tajacu</i> ¹
Fischer, 1814	<i>Tayassu pecari</i> ²	<i>Tayassu patira</i>
Illiger, 1815	<i>Sus albirostris</i>	<i>Sus tajassu</i>
Fischer, 1817	<i>Notophorous pecari</i> ³	<i>Notophorous patira</i> ³
Cuvier, 1817	<i>Dicotyles labiatus</i>	<i>Dicotyles torquatus</i> ²
Reichenbach, 1835		<i>Pecari torquatus</i>
Gray, 1868	<i>Dicotyles labiatus</i>	<i>Notophorous torquatus</i> ³
Merriam, 1901	<i>Tayassu (Oliosus) albirostris</i>	<i>Tayassu (Tayassu) tajacu</i>
Gill, 1902	<i>Tayassu pecari</i>	<i>Dicotyles torquatus</i>
Gidley, 1920	<i>Tayassu</i> ⁴	<i>Pecari</i> ⁴
Tate, 1939	<i>Tagassu pecari</i> ¹	<i>Tagassu tajacu</i> ¹
Frenchkop, 1955	<i>Tayassu pecari</i>	<i>Dicotyles tajacu</i>
Hall and Kelson, 1959	<i>Tayassu pecari</i>	<i>Tayassu tajacu</i>
This paper	<i>Tayassu pecari</i> Fischer, 1814	<i>Dicotyles tajacu</i> (Linnaeus, 1758)

¹Frisch's names are non-Linnaean.

²Genotypic species of *Tayassu* and *Dicotyles* respectively by reason of priority. A number of later authors considered that Gray (1868) "designated" *D. labiatus* as the type of *Dicotyles*. Gray lists *Dicotyles labiatus* as the white lipped peccary and *Notophorous torquatus* as the collared peccary, apparently replacing Cuvier's name for the latter with *Notophorous* Fischer, 1817. Furthermore, even if *Notophorous* were valid, its genotypic species would be *Notophorous* [= *Tayassu*] *pecari* Fischer (1814) which is the white lipped, not the collared peccary. On the basis of page priority in the original description (Cuvier, 1817), *D. torquatus* must surely be taken as the genotypic species of the Collared Peccary.

³*Notophorous* derives from Fischer (1817). Fischer attempted to replace *Tayassu* with *Notophorous*, but no generic or specific diagnoses were given. *Notophorous* is a junior synonym of *Tayassu*.

⁴Gidley gave diagnoses of the two genera but did not designate any species names.

